

# UC Irvine

## UC Irvine Previously Published Works

### Title

Diurnal patterns of leaf photosynthesis, conductance and water potential at the top of a lowland rain forest canopy in Cameroon: measurements from the Radeau des Cimes.

### Permalink

<https://escholarship.org/uc/item/0b14p61f>

### Journal

Tree Physiology, 14(4)

### ISSN

0829-318X

### Authors

Koch, GW  
Amthor, JS  
Goulden, ML

### Publication Date

1994-04-01

### DOI

10.1093/treephys/14.4.347

### Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

## Diurnal patterns of leaf photosynthesis, conductance and water potential at the top of a lowland rain forest canopy in Cameroon: measurements from the *Radeau des Cimes*

GEORGE W. KOCH,<sup>1</sup> JEFFREY S. AMTHOR<sup>2</sup> and MICHAEL L. GOULDEN<sup>3</sup>

<sup>1</sup> Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA

<sup>2</sup> Woods Hole Research Center, Woods Hole, MA 02543, USA

<sup>3</sup> Division of Applied Science and Department of Earth and Planetary Science, Harvard University, Cambridge, MA 02138, USA

Received May 26, 1993

### Summary

Diurnal patterns of leaf conductance, net photosynthesis and water potential of five tree species were measured at the top of the canopy in a tropical lowland rain forest in southwestern Cameroon. Access to the 40 m canopy was by a large canopy-supported raft, the *Radeau des Cimes*. The measurements were made under ambient conditions, but the raft altered the local energy balance at times, resulting in elevated leaf temperatures. Leaf water potential was equal to or greater than the gravitational potential at 40 m in the early morning, falling to values as low as  $-3.0$  MPa near midday. Net photosynthesis and conductance were typically highest during midmorning, with values of about  $10\text{--}12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $0.2\text{--}0.3 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , respectively. Leaf conductance and net photosynthesis commonly declined through midday with occasional recovery late in the day. Photosynthesis was negatively related to leaf temperature above midday air temperature maxima. These patterns were similar to those observed in other seasonally droughted evergreen communities, such as Mediterranean-climate shrubs, and indicate that environmental factors may cause stomatal closure and limit photosynthesis in tropical rain forests during the midday period.

*Keywords:* leaf conductance, net photosynthesis, stomatal conductance, tropical rain forest.

### Introduction

Despite the large area of tropical and subtropical wet-moist forest, i.e., about  $13 \times 10^6 \text{ km}^2$  (Olson et al. 1983), and the significance of canopy physiology to the mass and energy exchange of forest ecosystems, little is known about diurnal or seasonal patterns of leaf conductance and net photosynthesis and their relationships to the environment in tropical forest tree canopies. Difficulties with access to canopies has limited physiological research to seedlings, gap and understory plants, and low branches on tall trees; only a few studies have included the foliage at the top of the forest which dominates ecosystem mass and energy exchange processes.

The few published studies of tropical forest canopy-leaf conductance and photosynthesis have shown a variety of diurnal patterns that may be related to seasonal changes in water availability and microclimate. Midday canopy-leaf stomatal closure was detected during the annual dry period (about 135 mm rain per month) in *Cyrilla racemiflora* L. and *Clethra occidentalis* (L.) Kuntze in an upper montane rain forest (1550 m altitude) in the Blue Mountains of Jamaica during a day when leaf temper-

ature reached 32–34 °C, but not on another day when leaf temperature remained below 30 °C (Aylett 1985). Conductance of leaves from a premontane wet forest in Costa Rica did not show a midday decline during the dry season, although both irradiance and conductance were low (Oberbauer et al. 1987). Leaf conductance in several species showed midmorning peaks, followed by declines throughout the remainder of the day, near the top of the canopy in a *terra firme* forest in Brazil (Roberts et al. 1990). This pattern was especially evident under conditions of high light and vapor pressure deficit during the dry season. A marked reduction in conductance after midmorning was reported for canopy leaves of the emergent *Qualea rosea* Aubl. in French Guiana (Roy and Salager 1992).

Compared to conductance, there have been even fewer studies of tropical forest canopy-leaf net photosynthesis. *Argyrodendron peralatum* (F.M. Bailey) Edlin ex I.H. Boas canopy-leaf photosynthesis declined in midafternoon when light was still above a saturating PPFD in an Australian tropical forest during the dry season (Percy 1987). Percy noted that water vapor deficits, high leaf temperature and low leaf water potential may have contributed to slight stomatal closure and decreased photosynthesis. During the first two days after rain near the end of a prolonged dry season, leaf photosynthesis in the upper crown of the same *A. peralatum* studied by Percy closely tracked the diurnal course of light (Doley et al. 1988). During the third and fourth days after rain, however, photosynthesis declined sharply after midmorning and remained low throughout the remainder of the day. Canopy-leaf photosynthesis also declined after midmorning in *Qualea rosea* in French Guiana (Roy and Salager 1992). Ground-based fluorescence measurements indicated midday and afternoon photoinhibition and suggested photodamage to leaves of two of three species collected from the canopy of a dry Pacific forest in Panama, but *in situ* gas exchange rates were not measured (Parker et al. 1992). For exposed leaves of several canopy species in Panama, diurnal changes in photosynthesis were reported to be primarily a function of incident PPFD without a midday decline (Zotz and Winter 1993).

The paucity of available information on tropical canopy-leaf conductance and photosynthesis precludes generalizations and points to the need for additional work. Therefore, we measured environmental conditions and leaf photosynthesis, conductance and water potential at the top (about 40 m above the ground) of the canopy of a lowland tropical rain forest in Cameroon during the dry season. The primary objective of the study was to determine whether dry-season midday conditions cause stomatal closure and inhibit photosynthesis. The study was made possible by the *Radeau des Cimes*, a unique dirigible-raft system developed by Hallé (1990) and his colleagues and used previously in forests of French Guiana (Hallé and Blanc 1990). A secondary objective of the study was to evaluate the *Radeau des Cimes* as a platform for research on canopy ecophysiology in tropical rain forests.

## Materials and methods

### *Study site and access to the canopy*

This study was part of the 1991 scientific expedition of *Opération Canopée* to the Campo wildlife reserve in southwestern Cameroon (2°09′–2°53′ N, 9°48′–10°25′ E). The reserve is a dense Guinea–Congo wet tropical lowland forest, part of the Cameroon–Congo evergreen sector of the Biafra Atlantic district. Mean annual precipitation is about 2500 mm, with a “dry” season extending from about mid-October through January during which monthly mean precipitation is approximately 100 mm. We made measurements during the periods November 19–22 and 26–28, 1991 (i.e., DOY [day of the year] 323–326 and 330–332). Rainfall during the period was high; about 140 mm of rain fell during the second half of November.

Access to the canopy was from the *Radeau des Cimes*, a large raft constructed of inflatable pontoons connected with Kevlar netting, which was placed on top of the forest canopy by means of a hot air dirigible (Hallé 1990). Once in place, the raft was supported by the canopy branches and provided a stable working platform of about 650 m<sup>2</sup> with a perimeter of about 90 m. Access to the raft was by a rope extended to the ground.

We studied top-of-the-canopy leaves at two raft locations. During the period DOY 323–326, the raft was supported by trees of *Dialium pachyphyllum* Harms (Caesalpiaceae) and *Sacoglottis gabonensis* (Baill.) Urban (Humiriaceae) at a site hereafter called Location 1. During the period DOY 330–332, the raft was supported mainly by a large *Piptadeniastrum africanum* (Hook. f.) Brenan (Mimosaceae) tree about 2 km from Location 1 at a site hereafter called Location 2. At both locations, the raft was positioned in the uppermost canopy, about 40 m above the ground, and several other species were located around the raft's perimeter. The crown supporting the raft was compressed and suffered some broken branches; however, numerous intact unshaded branches of the supporting and nearby trees were accessible from the raft's perimeter and such branches were used in this study.

Leaf photosynthesis, conductance, and water potential measurements were obtained for five species: *D. pachyphyllum*, *S. gabonensis*, *Irvingia grandiflora* Hook. f. (Irvingiaceae), *Strophanthus* DC. sp. (Apocynaceae), and *Hymenostegia afzelli* (Oliv.) Harms (Caesalpiaceae). Descriptions of some of the species studied and others encountered during the expedition are in Hallé and Pascal (1992).

### *Environmental monitoring*

Incident photosynthetic photon flux density (PPFD), net radiation, air and canopy temperatures, and relative humidity were continuously measured from the end of a fiberglass boom extending about 2 m above and about 3 m away from the edge of the raft with a silicon quantum sensor (Li-Cor, Lincoln, NE, USA), a thermopile net radiometer (Kahl Scientific Instruments, El Cajon, CA, USA), shaded fine wire thermocouples, an infrared radiometer (Everest Interscience) positioned to view about 0.25 m<sup>2</sup> of the canopy, and a ventilated psychrometer. Instrument outputs were scanned every 5 s and means were stored every 600 s using a solid state data logger

(Campbell 21X, Campbell Scientific, Logan, UT, USA). The infrared radiometer monitored mainly leaves of a *D. pachyphyllum* tree at Location 1 and leaves of the *P. africanum* at Location 2.

#### *Leaf water potential, stomatal conductance, and apparent photosynthesis*

Water potential, conductance and photosynthesis were measured for mature leaves on the outer portion of a branch that showed no obvious signs of previous damage, such as tears or herbivory. Leaf water potential was measured with a Scholander pressure chamber (PMS, Corvallis, OR, USA). Leaves less than 1 m from the raft, generally from the same sub-crown on which leaf gas exchange measurements were made, were arbitrarily collected and promptly placed in the chamber. Chamber pressure was increased at less than  $0.1 \text{ MPa s}^{-1}$ . Xylem water potential of *D. pachyphyllum* leaves was monitored throughout the day on DOY 324 and 325. On DOY 330 and 331, leaves of all five species were measured periodically during the day. Four to six leaves were measured about every 2 h.

Two cross-calibrated portable gas exchange systems (Model LI-6200, Li-Cor, Lincoln, NE, USA) were used to monitor  $\text{CO}_2$  and  $\text{H}_2\text{O}$  exchange of intact leaves. The capacitance-type water vapor sensors used in the LI-6200 often show a nonlinear response and hysteresis at relative humidity above 80% (Pearcy et al. 1989). This was a potentially important source of error in measurements of leaf conductance and leaf intercellular  $\text{CO}_2$  partial pressure ( $C_i$ ) early in the morning when relative humidity was high, but of negligible significance to measurements of photosynthesis.

At Location 1, gas exchange measurements were made on mature, unshaded leaves from several branches of *D. pachyphyllum*. At Location 2, four to six leaves of each of the five species were labeled at the base of the petiole and monitored repeatedly over the course of DOY 330 and 331.

#### *Leaf chemistry*

The leaves used for gas exchange measurements and leaves of other species were collected and dried at  $50 \text{ }^\circ\text{C}$ . Leaf nitrogen content was determined by the Kjeldahl method (Isaac and Johnson 1976). Leaf  $^{13}\text{C}/^{12}\text{C}$  ratios were determined by mass spectrometry (Tieszen et al. 1979) at the National Science Foundation Isotope Laboratory at the University of Utah, Salt Lake City, Utah.

## **Results and discussion**

### *Environmental conditions*

Conditions at the top of the canopy were warm and humid with partly cloudy skies and occasional heavy rains (Figure 1). PPFD approached  $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and net radiation exceeded  $700 \text{ W m}^{-2}$  under clear sky conditions. Air temperature increased from a minimum of about  $22\text{--}23 \text{ }^\circ\text{C}$  around sunrise to near  $30 \text{ }^\circ\text{C}$  in the early afternoon. During the late afternoon temperature decreased rapidly, but during the



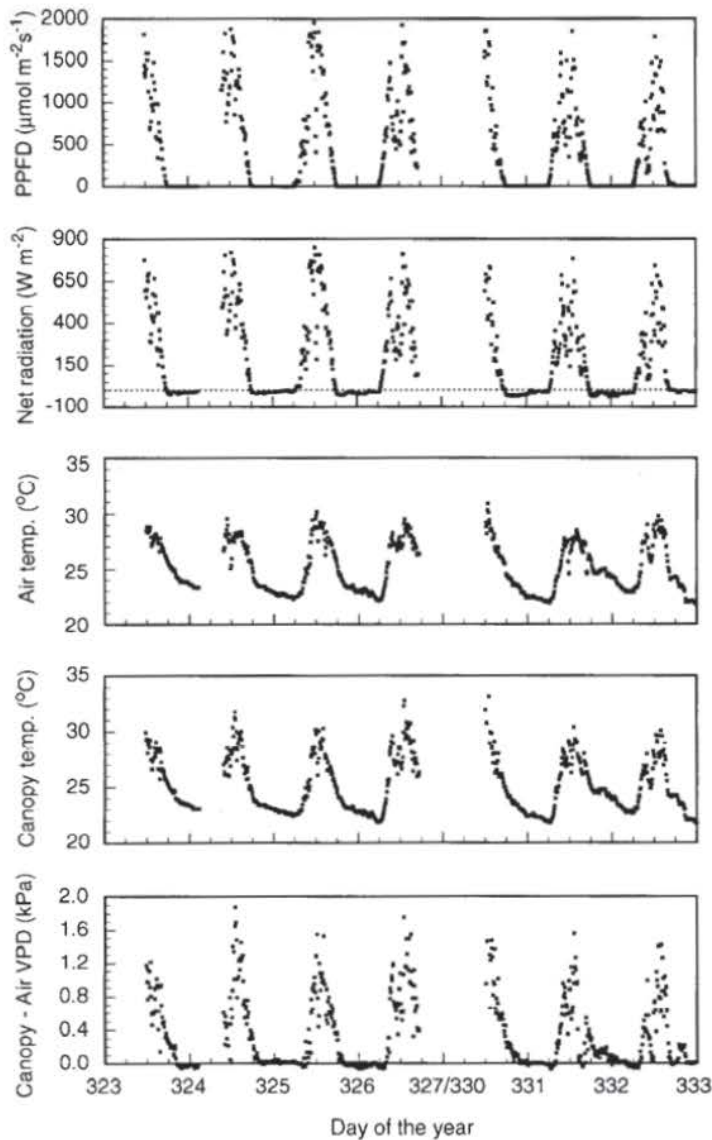


Figure 1. Environmental conditions above the canopy at Locations 1 and 2. Shown are 10-min mean values of PPFD, net radiation, air temperature, canopy temperature and canopy–air vapor pressure difference. The sensor array was on a boom about 2 m above and 3 m away from the raft. Note the break in the abscissa after DOY 326, i.e., 2400 h on DOY 326 shares the tick mark with 0000 h on DOY 330.

night temperature decreased more slowly. Relative humidity was near 100% during the night and decreased to 70–80% during the midday period, whereas the dewpoint was relatively constant over the diel cycle. At the base camp, about 2 km from Locations 1 and 2, precipitation of more than 10 mm was measured on DOY 321, 322, 324 and 329, and lesser amounts of rain occurred on an additional 4 days during

### Leaf water potential

Upper canopy leaves of *D. pachyphyllum* showed a pronounced diurnal cycle in water potential that was inversely related to the pattern of variation of leaf temperature and leaf-air vapor pressure difference (VPD) (Figures 2a-c). Early in the

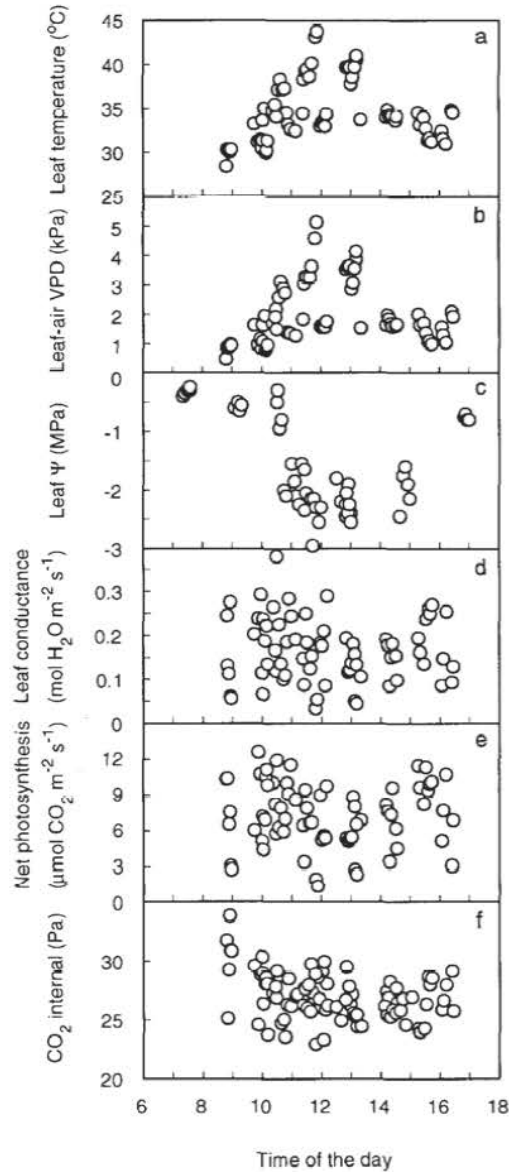


Figure 2. Diurnal course of leaf temperature, leaf-air vapor pressure difference (VPD), leaf water potential ( $\Psi$ ), leaf conductance, leaf net photosynthesis and intercellular  $\text{CO}_2$  partial pressure for leaves of *D. pachyphyllum* measured at the top of the canopy on DOY 323, 324 and 325 (pooled). Leaves within 1.0 m of the raft were collected and measured immediately for water potential. All data except some early

morning, water potential was high, i.e.,  $-0.40$  to  $-0.25$  MPa. Leaf water potential declined sharply after 0900 h concomitant with increasing leaf and air temperatures and leaf–air VPD. Measurements made on the five species, including *D. pachyphyllum*, at Location 2 on DOY 331 and 332 were quantitatively similar (data not shown) to those of *D. pachyphyllum* at Location 1 although fewer measurements per species were obtained.

The diurnal pattern of leaf water potential and the midday values of  $-2.5$  to  $-2.0$  MPa were similar to those of evergreen sclerophyllous canopy leaves in an Australian tropical forest during the dry season (Pearcy 1987). The early morning leaf water potential of *D. pachyphyllum* at Location 1 (Figure 2c) and that of three species at Location 2 on DOY 330 (data not shown) were slightly greater (less negative) than the value ( $-0.39$  MPa) required to lift water 40 m to the top of the canopy. Because the canopy leaves were wet during the night and early morning, it is possible that water uptake occurred through leaves and branches in the canopy allowing a leaf water potential greater than the gravitational potential.

#### *Leaf conductance and photosynthesis*

A pooled response curve of the several hundred measurements of leaf gas exchange suggested that PPFD was not a major limitation to conductance or photosynthesis when PPFD incident on the leaves was at least  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$  (data not shown). (PPFD incident on individual leaves more or less facing the sun exceeded PPFD incident on the canopy.) Similar findings have been reported by Pearcy (1987), Doley et al. (1988), and Zotz and Winter (1993). Many sets of measurements made at PPFD  $\geq 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  were, therefore, pooled and are presented together.

Leaf conductance of *D. pachyphyllum* on DOY 323, 324 and 325 showed a slight midday depression for measurements made with PPFD  $\geq 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 2d). Mean values  $\pm$  SE of leaf conductance before 1100 h ( $= 0.19 \pm 0.02 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) and after 1500 h ( $= 0.18 \pm 0.02 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) were higher than the mean for the 1100–1500 h period ( $= 0.14 \pm 0.01 \text{ mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ). A similar weak, but significant relationship between leaf net photosynthesis and time of day on DOY 323, 324 and 325 was apparent for *D. pachyphyllum* leaves measured with incident PPFD  $\geq 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 2e). As was the case for conductance, mean values  $\pm$  SE of photosynthesis before 1100 h ( $= 8.1 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ ) and after 1500 h ( $= 8.8 \pm 0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ ) were similar and were both significantly greater than the values during the 1100–1500 h period ( $= 6.2 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ ). Diurnal patterns of conductance and photosynthesis for *D. pachyphyllum* and the four other species examined on DOY 330 and 331 were qualitatively similar to those shown for *D. pachyphyllum* on DOY 323, 324 and 325, with maxima typically occurring before 1100 h (data not shown).

There was a slight but significant reduction in  $C_i$  during the course of the photo-period in *D. pachyphyllum* on DOY 323, 324 and 325 (Figure 2f;  $C_i = 31.6 - 0.38 \times$  hour of day,  $r = 0.375$ ,  $P = 0.0002$ ). Daytime values were always highest in the early



at midday. The trend of decreasing  $C_i$  throughout the light period was significant without the early morning (before 0930 h) values, but showed a more gradual decrease with time ( $C_i = 29.2 - 0.21 \times \text{hour of day}$ ,  $r = 0.219$ ,  $P = 0.04$ ). The midday decrease in  $C_i$  approximately paralleled the decrease in conductance. Along with the observed close correlation between photosynthesis and conductance (see below), this indicates that the midday decrease in photosynthesis was related to stomatal closure rather than to a biochemical limitation on photosynthesis.

Photosynthesis and conductance of *D. pachyphyllum* leaves were tightly coupled at incident PPFD  $\geq 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 3), similar to relationships observed under steady state conditions (e.g., Wong et al. 1985). A similar relationship between photosynthesis and conductance was observed during DOY 330 and 331 when all measurements from *I. grandiflora*, *Strophanthus* sp., and *H. afzelli* were pooled, whereas *Sacoglottis gabonensis* had a more constant photosynthetic rate across a wide range of conductance values (data not shown).

Photosynthesis and conductance in *D. pachyphyllum* were negatively related to leaf-air VPD and leaf temperature at incident PPFD  $\geq 500 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 4). Individual regressions of photosynthesis and conductance on leaf temperature and leaf-air VPD were all significant ( $P < 0.006$ ), although the correlation coefficients were small ( $r^2 < 0.17$  in all cases). Multiple regression of conductance on leaf-air VPD and leaf temperature resulted in a significant effect of VPD ( $P = 0.03$ ), but not temperature, indicating that the effect of temperature on conductance was manifest through an increase in VPD. A multiple regression of photosynthesis on leaf temperature, leaf-air VPD and leaf conductance resulted in a significant effect of conductance only, suggesting that the effects of VPD and temperature on photosynthesis were mediated by changes in conductance, which is consistent with the observed tight coupling of photosynthesis and conductance (Figure 3).

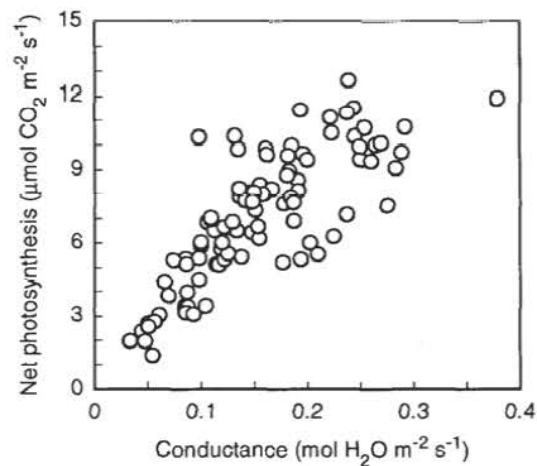


Figure 3. Net photosynthesis as a function of conductance for *D. pachyphyllum* leaves at the top of the canopy near the raft perimeter on DOY 323, 324 and 325. Data are for leaves exposed to incident PPFD

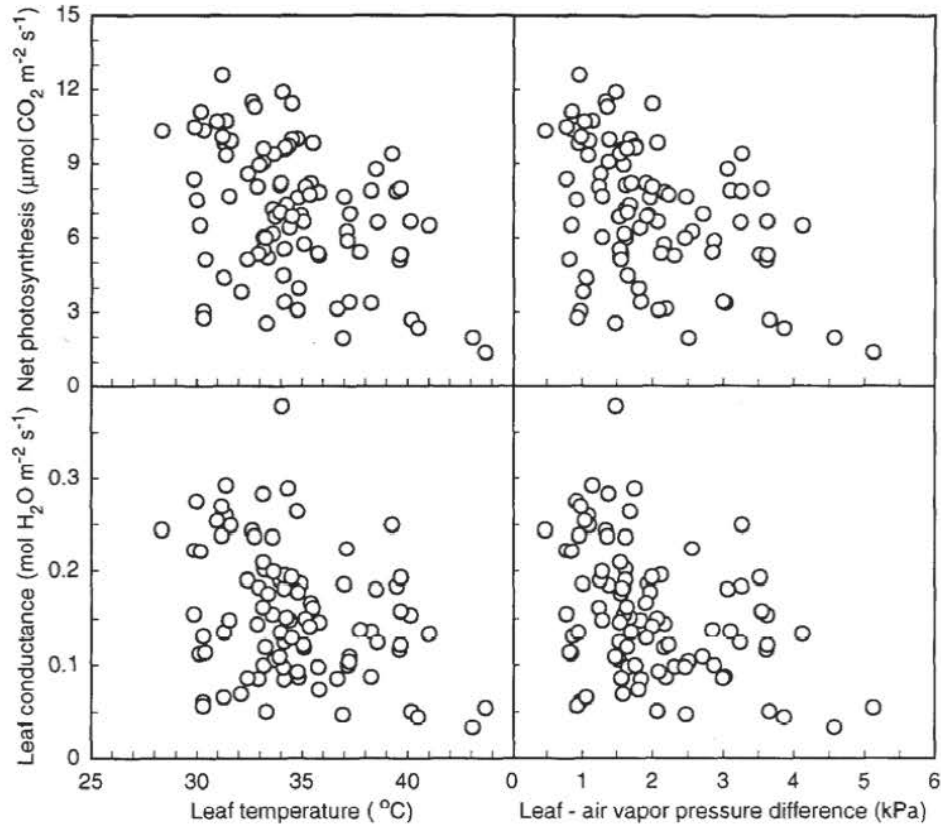


Figure 4. Net photosynthesis and conductance as a function of leaf temperature and leaf-air vapor pressure difference for *D. pachyphyllum* leaves at the top of the canopy on DOY 323, 324 and 325. Data are for leaves exposed to incident PPFD  $\geq 500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . See text for regression analyses.

These observations indicated a midday reduction in conductance and net  $\text{CO}_2$  uptake that was temporally correlated with increasing VPD, low leaf water potential, high air and leaf temperatures, and a decrease in  $C_a$ . As discussed below (see *Leaf temperature*), proximity to the raft apparently caused leaf warming that might have induced stomatal closure and inhibited photosynthesis. Top-of-the-canopy  $C_a$  exceeded 38 Pa before 0900 h, presumably resulting from the storage of respired  $\text{CO}_2$  in the canopy air space during atmospherically stable periods at night and early in the day (cf. Wofsy et al. 1988), and declined to less than 35 Pa by midday. An increase in  $C_a$  from 35 to 38 Pa should increase net photosynthesis by about 5% for typical  $C_3$  leaves (e.g., Farquhar and Wong 1984). The observed higher photosynthesis in the morning compared to midday still holds, however, when photosynthesis values are normalized for the effect of higher  $\text{CO}_2$  or if measurements made at  $C_a > 38$  Pa are excluded from the analysis (not shown).

Maximal rates of photosynthesis measured near the raft were generally similar to those measured near the canopy edge for *A. spongatum* (Poore 1997).

Doley et al. 1988) and *Ceiba petandra* (L.) Gaertn. (Zotz and Winter 1993), and midmorning conductance was similar to the few maximum values reported for other tropical forest canopy leaves (references cited in Introduction). These rates of canopy-leaf photosynthesis coupled with a canopy LAI estimated to be 4–6 suggest canopy and whole-forest CO<sub>2</sub> exchange rates consistent with the few previous observations in tropical forests, i.e., mean values of 18–21  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Lemon et al. 1970, Wofsy et al. 1988, Fan et al. 1990).

The measured diurnal patterns of leaf conductance and photosynthesis of canopy leaves in this lowland tropical rain forest of Cameroon were qualitatively similar to observations made in Mediterranean-climate ecosystems and in other hot, dry environments. In such environments, conductance and photosynthesis may also reach maximum values in the morning followed by a midday depression with perhaps a slight increase near the end of the day (e.g., Schulze and Hall 1982). Presumably, the diurnal patterns of leaf conductance and photosynthesis observed both in Mediterranean-climate ecosystems and at the top of the canopy in this tropical forest reflect either direct effects of water stress or are associated with strategies to maximize water use efficiency (Cowan 1982).

#### Leaf characteristics

Among the eight species sampled, the mean area of leaves at the top of the canopy varied from 19 to 148 cm<sup>2</sup>, specific leaf mass (SLM) ranged from 83 to 160 g m<sup>-2</sup>, and leaf nitrogen content varied from 113 to 230 mmol m<sup>-2</sup> (Table 1). These values of SLM and leaf nitrogen are typical of moist tropical forests on moderately infertile soils (Medina 1984, Vitousek and Sanford 1986 and references therein).

Leaf  $\delta^{13}\text{C}$  values ranged from -27.3 to -28.0‰ for the five species studied with respect to gas exchange and ranged from -27.6 to -30.3‰ for the other three species sampled (Table 1). These values are typical of C<sub>3</sub> leaves and indicate a  $C_i/C_a \approx 0.7$  (Farquhar et al. 1982), an average weighted for the photosynthetic rate during the periods when present leaf carbon was assimilated. It is noted that leaf structural

Table 1. Characteristics of leaves at the top of the canopy in a lowland rain forest in Cameroon. Values are means of three leaves for  $\delta^{13}\text{C}$  isotope composition and four to six leaves for other variables.

Species	Area (cm <sup>2</sup> )	Specific leaf mass (g m <sup>-2</sup> )	Nitrogen content (mmol m <sup>-2</sup> )	$\delta^{13}\text{C}$ (‰)
<i>Dialium pachyphyllum</i> <sup>1</sup>	25	160	172	-27.7
<i>Sacoglottis gabonensis</i> <sup>1</sup>	25	138	113	-28.0
<i>Irvingia grandiflora</i> <sup>1</sup>	148	106	151	-27.8
<i>Strophanthus</i> sp. <sup>1</sup>	18	119	159	-27.3
<i>Hymenostegia afzelli</i> <sup>1</sup>	37	83	149	-27.6
<i>Cnestis ferruginea</i> <sup>2</sup>	30	158	230	-30.3
<i>Mitragyna ciliata</i> <sup>2</sup>	130	120	126	-27.9
Unidentified <sup>2</sup>	19	107	208	-28.2

<sup>1</sup> Leaves used for gas exchange measurements at Location 1 or 2.

<sup>2</sup> Other leaves collected on top of the canopy.

carbon and carbon in nonstructural carbohydrates arose from photosynthesis occurring at different times. The apparent water use efficiency was neither unusually high nor unusually low. The  $\delta^{13}\text{C}$  values were also similar to the few previous reports for tropical forest canopy leaves. For example, upper canopy leaves of five species in a laterite Amazon rain forest in southern Venezuela had  $\delta^{13}\text{C}$  values of  $-26.4$  to  $-30.2\text{‰}$  and leaves of four canopy species at a podsol site had  $\delta^{13}\text{C}$  values of  $-28.8$  to  $-31.8\text{‰}$  (Medina and Minchin 1980). For mature leaves of six canopy species in a Puerto Rican montane forest,  $\delta^{13}\text{C}$  ranged from  $-27.6$  to  $-30.3\text{‰}$  (Medina et al. 1991). Leaves of three species from the canopy top in a Chinese monsoonal subtropical forest had  $\delta^{13}\text{C}$  values of about  $-28$  to  $-31\text{‰}$  (Ehleringer et al. 1986).

#### *Leaf temperature*

After several days of field measurements, it was apparent that, during the day, leaf temperatures adjacent to the raft were higher than both the ambient air temperature measured at the end of the environmental monitoring boom and the canopy temperature as measured with the infrared radiometer (Figure 1). High leaf temperatures appeared to be associated with reduced leaf photosynthesis.

To gauge the effect of the raft on leaf temperature, and by inference on leaf conductance and photosynthesis, fine wire thermocouples were attached to the lower surface of *D. pachyphyllum* leaves at various distances from the raft. Two sets of five leaves each (using parallel thermocouples) that were within 1.0 m of the raft were compared with a third group of five leaves that was 1.5–2.0 m from the raft. The average temperature of each group of five leaves was logged simultaneously with the environmental conditions, including air and canopy temperature, from about noon on DOY 331 until after sunset on DOY 332.

Leaf temperatures 1.5–2.0 m from the raft were generally within 1 °C of ambient air temperature, never exceeded air temperature by as much as 2 °C, and were often below air temperature (data not shown). On the whole, leaf thermocouple measurements 1.5–2.0 m from the raft agreed closely with the infrared radiometer estimates of canopy temperature during the same period (IR radiometer =  $1.003 \times$  thermocouple  $- 0.049$  (in °C),  $r^2 = 0.971$ ). Leaf temperature less than 1.0 m from the raft closely matched those at 1.5–2.0 m from the raft at temperatures below 25 °C, but above this temperature, the leaves nearer the raft were considerably warmer than those more distant (Figure 5).

The greater leaf temperatures near the raft were presumably a result of local sensible and radiative heat flux from the pontoons. As a consequence, leaves near the raft may have been warmed to temperatures above those to which they were acclimated, resulting in a significant midday high temperature stress and consequently, a reduction in conductance and photosynthesis. This was consistent with the observation of Aylett (1985) that midday stomatal closure occurred when leaf temperature was 32–34 °C, but not when leaf temperature was 30 °C. Thus, although we are confident that midday stomatal closure occurs at leaf temperatures above 33–35 °C, without a long-term record of canopy temperature we are unable to quantify the degree to which temperature induced stomatal closure might limit

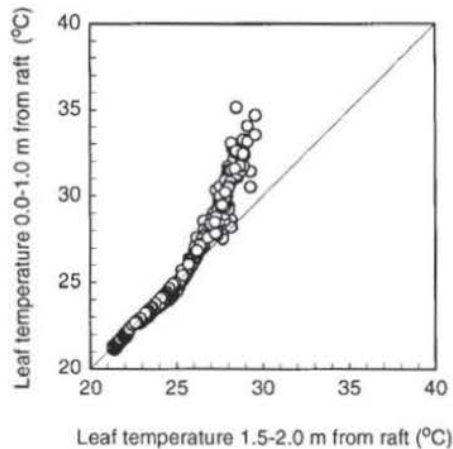


Figure 5. Temperature of *D. pachyphyllum* leaves located 0.0–1.0 m versus leaves located 1.5–2.0 m from an outer pontoon of the canopy raft. Values at 0.0–1.0 m are the means of two sets of five leaves each (measured with parallel fine wire thermocouples) and those at 1.5–2.0 m are for a single set of five leaves. Measurements were logged every 10 min during the period from about noon on DOY 331 to after sunset on DOY 332.

annual carbon assimilation. A more complete analysis could be achieved with detailed studies of leaf energy exchange, photosynthesis, conductance and water potential at the top of the canopy within controlled environment cuvettes.

### Conclusions

The *Radeau des Cimes* system (Hallé 1990) afforded excellent access to the top of the canopy for studies of *in situ* leaf photosynthesis, conductance and water potential. In contrast to scaffolding towers, several species and individuals could be studied at one time under relatively comfortable and stable working conditions—access to leaves is potentially available along the entire perimeter (90 m) of the raft. In this study, we had access to eight species at two raft locations and five species were examined with respect to leaf physiology. The diurnal patterns and magnitudes of leaf photosynthesis, conductance and water potential were consistent with the limited literature for wet tropical forest canopies. Maximum values of photosynthesis and conductance were  $10\text{--}12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $0.2\text{--}0.3 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ , respectively, and were reached during early- to midmorning. Photosynthesis and conductance decreased during midday in association with daily maxima in air and leaf temperatures and leaf–air VPD, and minimum values of leaf water potential. The major difficulty encountered in our study was the apparent altered energy balance and temperature of leaves near the raft. We contend that the observed post-morning decreases in leaf conductance and net photosynthesis were at least partly due to high temperature stress of leaves in proximity to the raft; we cannot be certain how leaves distant from the raft responded to ambient midday environmental conditions. This



Not only do leaf-chambers alter the leaf environment, but gaining access to the canopy, by whatever means, including the raft, scaffolding towers, cranes or ropes, can alter the microclimate of leaves and has the potential to perturb normal leaf processes. This needs to be explicitly addressed when studying leaf processes in the field. A combination of approaches with controlled-environment and transient ambient gas exchange techniques, non-invasive methods such as stem flux and eddy covariance, and remotely-sensed indices of canopy activity will improve understanding of leaf physiology of tropical forest canopies.

#### Acknowledgments

We thank Foundation ELF for supporting our contribution to the 1991 expedition of *Opération Canopée*. We are also grateful for the excellent logistical and technical support and camaraderie provided by Francis Hallé and the crew of *Opération Canopée*. We thank Jacques Roy for inspiration for this study and Jean-Louis Salager for his assistance with water potential measurements.

#### References

- Aylett, G.P. 1985. Irradiance interception, leaf conductance and photosynthesis in Jamaican upper montane rain forest trees. *Photosynthetica* 19:323–337.
- Cowan, I.R. 1982. Regulation of water use in relation to carbon gain in higher plants. In *Physiological Plant Ecology II: Water Relations and Carbon Assimilation*. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer Verlag, Berlin, pp 589–613.
- Doley, D., G.L. Unwin and D.J. Yates. 1988. Spatial and temporal distribution of photosynthesis and transpiration by single leaves in a rain forest tree, *Argyrodendron perlatum*. *Aust. J. Plant Physiol.* 15:317–326.
- Ehleringer, J.R., C.B. Field, Z. Lin and C. Kuo. 1986. Leaf carbon isotope and mineral composition in subtropical plants along an irradiance cline. *Oecologia* 70:520–526.
- Fan, S.-M., S.C. Wofsy, P.S. Bakwin, D.J. Jacob and D.R. Fitzjarrald. 1990. Atmosphere–biosphere exchange of CO<sub>2</sub> and O<sub>3</sub> in the central Amazon Basin. *J. Geophys. Res.* 95:16851–16864.
- Farquhar, G.D. and S.C. Wong. 1984. An empirical model of stomatal conductance. *Aust. J. Plant Physiol.* 11:191–210.
- Farquhar, G.D., M.H. O'Leary and J.A. Berry. 1982. On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9:121–137.
- Hallé, F. 1990. A raft atop the rain forest. *Nat. Geograph.* 178:128–138.
- Hallé, F. and P. Blanc. 1990. *Biologie d'une canopée de forêt équatoriale*. Fondation ELF, Paris, 231 p.
- Hallé, F. and O. Pascal. 1992. *Biologie d'une canopée de forêt équatoriale—II*. Fondation ELF, Paris, 288 p.
- Isaac, R.A. and W.C. Johnson. 1976. Determination of total nitrogen in plant tissue using a block digester. *J. Assoc. Anal. Org. Chem.* 59:98–100.
- Lemon, E., L.H. Allen, Jr. and L. Müller. 1970. Carbon dioxide exchange of a tropical rain forest. Part II. *BioScience* 20:1054–1059.
- Medina, E. 1984. Nutrient balance and physiological processes at the leaf level. In *Physiological Ecology of Plants of the Wet Tropics*. Eds. E. Medina, H.A. Mooney and C. Vásquez-Yanes. Dr. W. Junk Publishers, The Hague, pp 139–154.
- Medina, E. and P. Minchin. 1980. Stratification of  $\delta^{13}\text{C}$  values of leaves in Amazonian rain forests. *Oecologia* 45:377–378.
- Medina, E., L. Sternberg and E. Cuevas. 1991. Vertical stratification of  $\delta^{13}\text{C}$  values in closed natural and plantation forest in the Luquillo mountains, Puerto Rico. *Oecologia* 87:369–372.
- Oberbauer, S.F., B.R. Strain and G.H. Riechers. 1987. Field water relations of a wet-tropical forest tree species, *Pentaclethra macroleoba* (Mimosaceae). *Oecologia* 71:369–374.
- Olson, J.S., J.A. Watts and L.J. Allison. 1983. Carbon in live vegetation of major world ecosystems. ORNL-5862. Oak Ridge National Lab., Oak Ridge, TN, 180 p.



- Parker, G.G., A.P. Smith and K.P. Hogan. 1992. Access to the upper forest canopy with a large tower crane. *BioScience* 42:664–670.
- Pearcy, R.W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. *Funct. Ecol.* 1:169–178.
- Pearcy, R.W., E.-D. Schulze and R. Zimmermann. 1989. Measurement of transpiration and leaf conductance. *In* *Plant Physiological Ecology: Field Methods and Instrumentation*. Eds. R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman and Hall, London, pp 137–160.
- Roberts, J., O.M.R. Cabral and L.F. de Aguiar. 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. *J. Appl. Ecol.* 27:336–353.
- Roy, J. and J.-L. Salager. 1992. Midday depression of net CO<sub>2</sub> exchange of leaves of an emergent rain forest tree in French Guiana. *J. Trop. Ecol.* 8:499–504.
- Salager, J.-L., G.W. Koch, J.S. Amthor, M.L. Goulden and J. Halatas. 1992. Données microclimatiques en forêt tropicale du sud Cameroun. *In* *Biologie d'une Canopée de Forêt Équatoriale—II*. Eds. F. Hallé and O. Pascal. Fondation ELF, Paris, pp 264–270.
- Schulze, E.-D. and A.E. Hall. 1982. Stomatal responses, water loss and CO<sub>2</sub> assimilation rates of plants in contrasting environments. *In* *Physiological Plant Ecology II: Water Relations and Carbon Assimilation*. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, Berlin, pp 181–230.
- Tieszen, L.L., D. Hein, S.H. Qvotrop, J.H. Troughton and S.K. Imbamba. 1979. Use of  $\delta^{13}\text{C}$  values to determine vegetation selectivity in east African herbivores. *Oecologia* 37:351–359.
- Vitousek, P.M. and R.L. Sanford. 1986. Nutrient cycling in moist tropical forest. *Annu. Rev. Ecol. Syst.* 17:137–167.
- Wofsy, S.C., R.C. Harriss and W.A. Kaplan. 1988. Carbon dioxide in the atmosphere over the Amazon Basin. *J. Geophys. Res.* 93:1377–1387.
- Wong, S.-C., I.R. Cowan and G.D. Farquhar. 1985. Leaf conductance in relation to rate of CO<sub>2</sub> assimilation. I. Influence of nitrogen nutrition, phosphorus nutrition, photon flux density and ambient partial pressure of CO<sub>2</sub> during ontogeny. *Plant Physiol.* 78:821–825.
- Zotz, G. and Winter, K. 1993. Short-term photosynthesis measurements predict leaf carbon balance in tropical rain forest canopy plants. *Planta* 191:409–412.