

VERTICAL PROFILES IN A BRUNEI RAIN FOREST: I. MICROCLIMATE ASSOCIATED WITH A CANOPY TREE

Martin G. Barker*

Department of Botany, University of Florida, Gainesville, FL 32611-8526, United States of America

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BARKER, M.G. 1996. Vertical profiles in a Brunei rain forest: I. Microclimate associated with a canopy tree. The microclimate variables, carbon dioxide (CO₂) concentration, air temperature, relative humidity and photon flux density (PFD), were measured in a vertical profile of rain forest in Brunei associated with a *Dryobalanops lanceolata* canopy tree. This descriptive study of vertical microclimate was conducted to answer the questions: what specific microclimate can leaves occupying different height positions be expected to experience diurnally, and what are the physiological implications of microclimate differences? Measurements were made at 1-m intervals between the understory (at 1 m) and the upper canopy (at 34 m), during the morning (0800-1100 h), mid-day (1100-1400 h), and afternoon (1500-1700 h) during three non-consecutive days. Understory CO₂ concentrations were high, but only at 1 m and only during one morning; thus, the hypothesis that the availability of CO₂ for photosynthesis is greater in the understory than elsewhere in the profile was not supported in this study. Temperature and vapour pressure deficit data suggest an afternoon "inversion surface" beneath the main canopy. During mid-day and afternoon in the upper part of the canopy, steep gradients of PFD were detected, and PFD was relatively high in the mid-canopy. A case is argued for more extensive and intensive studies, in conjunction with investigations of above-ground spatial organisation of vegetation, to provide information on vertical resource-utilisation by plants.

Key words: Canopy - CO₂ - diurnal - light - photon flux density - relative humidity - temperature - understory - vapour pressure deficit - vertical profile

BARKER, M.G. 1996. Profil tegak di sebuah hutan hujan di Brunei: I. Mikroiklim yang berkaitan dengan dengan pokok sudur. Pembolehubah mikroiklim, kepekatan karbon dioksida (CO₂), suhu udara, kelembapan relatif dan ketumpatan fluks foton (PFD), disukat di dalam profil tegak sebuah hutan hujan di Brunei yang berkaitan dengan pokok sudur *Dryobalanops lanceolata*. Kajian secara deskriptif mengenai mikroiklim tegak dijalankan untuk mendapatkan jawapan-jawapan bagi soalan-soalan berikut: apakah jenis mikroiklim yang dijangka akan dialami sehari oleh daun yang berada pada ketinggian berbeza, dan apakah implikasi-implikasi fisiologi di dalam perbezaan-perbezaan mikroiklim? Ukuran-ukuran dibuat pada selang 1-m di antara understorey (pada 1 m) dan sudur atas (pada 34 m), pada waktu pagi (0800-1100 h), tengah hari (1100-1400 h), dan petang (1500-1700 h) tiga hari berturut-turut. Kepekatan CO₂ understorey adalah tinggi, tetapi hanya pada 1 m dan hanya pada satu pagi; oleh yang demikian, hipotesis bahawa bekalan CO₂ untuk fotosintesis adalah lebih tinggi di dalam understorey daripada di tempat-tempat lain di dalam profil adalah tidak disokong di dalam kajian ini. Suhu dan tekanan wap data defisit mengesyorkan

*Present address: Top Bol 5053, P.O. Box 520777, Miami, FL 33152-0777, U.S.A.

Address after 31 August 1996: Department of Forestry, MacRobert Building, University of Aberdeen, Aberdeen AB24 5UA, U.K.

“penyongsangan permukaan” petang di bawah sudur utama. Pada waktu tengah hari dan petang, di bahagian atas sudur, kecuraman cerun PFD telah dikesan di bahagian atas sudur, dan PFD adalah tinggi secara relatif di dalam sudur tengah. Satu kes dipertikaikan bagi menjalankan kajian yang lebih meluas dan mendalam, sempena dengan kaji selidik mengenai susunan ruang tumbuh-tumbuhan di atas tanah, bagi membekalkan maklumat mengenai penggunaan-sumber tegak oleh tumbuh-tumbuhan.

Introduction

Considerable spatial and temporal variabilities exist in tropical forest microclimate (e.g. Kira & Yoda 1989, Fitzjarrald & Moore 1995). The vertical pattern of microclimate parameters is potentially important in determining the distribution of species (e.g. Terbough 1985) and biomass (e.g. Ardhana *et al.* 1988). Stratification, a characteristic of tropical rain forests, results from uneven vertical arrangements of species, individuals at different developmental stages, and leaf mass (Bourgeron 1983, Koike & Syahbuddin 1993). The arrangement of vegetation affects within-canopy processes such as evapotranspiration, CO₂ fluxes and light interception (Lemon *et al.* 1970, Koike & Syahbuddin 1993, McWilliam *et al.* 1993). Hence, additional heterogeneity produced by the growth and canopy structure of individual plants themselves contributes to habitat microclimate characteristics (Field 1988).

The vertical distribution of forest microclimate has received less attention than that in the ground-level horizontal plane. Differing ground-level microsites in the understory-gap continuum are highly accessible and microclimate gradients between them are often of considerable interest for plants at the seedling stage as well as ground-dwelling animals. In contrast, studies of microsites in the vertical plane present considerable difficulties for access (Kira & Yoda 1989, Barker & Sutton, *in press*), yet are also of considerable ecological importance.

Many plants and animals partly or exclusively occupy the portion of tropical rain forests above ground-level; vertical gradients in microclimate are likely to be important in affecting the distribution and functioning of these organisms. For example, Chazdon (1986) showed that in the vertical gradients of light near the rain forest floor in Costa Rica, some palms were functioning above photosynthetic compensation whilst others were functioning below. Lower-canopy elements may have photosynthetic rates less than those of the upper canopy (see Lemon *et al.* 1970, Mooney *et al.* 1984, Ellsworth & Reich 1993). In some cases, it seems that plants can “forage” for light in the three-dimensional forest environment (Canham 1988, Castellanos *et al.* 1992). Such phenomena are likely to have important implications for carbon gain in canopy plants which grow up through vertical microclimate gradients during their development (see Oberbauer & Strain 1986). Any microclimate changes with height can, therefore, be expected to be accompanied by height-related differences in leaf characteristics (Ellsworth & Reich 1993, Gallego *et al.* 1994, Barker & Booth, *in press*) and, ultimately, the distribution of invertebrates which are often associated with leaves. For example, height-related variations in specific leaf area (Ellsworth & Reich 1993, McWilliam

et al. 1993) or leaf nitrogen content (Field 1988, Ellsworth & Reich 1993) might be expected to influence the vertical distribution of insect herbivores. Entire plants and associated fauna are also affected, such as epiphytes which segregate vertically along light and relative humidity gradients (Benzing 1995).

Despite the substantial practical difficulties in studying microclimate associated with tall tropical forests, the vertical distribution of microclimatic variables in tropical rain forests has been studied in Panamá (Smith *et al.* 1992), Trinidad (Broadmeadow *et al.* 1992), Costa Rica (Lemon *et al.* 1970), Brazil (Shuttleworth *et al.* 1985) and in Malaysia, at Pasoh (Aoki *et al.* 1978, Yoda 1978, Kira & Yoda 1989). However, no such studies have been previously conducted in Borneo. Microclimate parameters, including those in the vertical profile of tropical forests, have been extensively reviewed by Shuttleworth (1989). Previous investigations have tended to focus on single microclimate variables such as light or CO₂ concentration. Whilst light (referred to here as photon flux density, PFD) is the most variable microclimate component in the vertical forest profile (e.g. Chiariello 1984), there are still insufficient data of vertical gradients of light within or between different forests (Canham *et al.* 1990). Direct covariates of light are temperature, relative humidity and vapour pressure deficit, each of which is ecologically important and on which even fewer studies have been conducted than those for light.

In this paper, I present vertical profiles for five microclimate parameters associated with a canopy tree. I adopted a 'tree-centered', or 'dendrocentric' approach (*sensu* Lieberman *et al.* 1989) in contrast to tower-based methods used by several previous researchers (e.g. Lemon *et al.* 1970, Aoki *et al.* 1978, Shuttleworth *et al.* 1985, Eliás *et al.* 1989), which often do not provide complete intimate access to leaf environments (see Barker & Sutton, in press). There were two further reasons for using a dendrocentric approach. Firstly, because a narrow profile was used, any changes in microclimate could be mainly attributed to height rather than to horizontal heterogeneity (see Torquebiau 1988, Kira & Yoda 1989, Baldocchi & Collineau 1994); horizontal heterogeneity often increases with height, for example due to the fact that forest gaps are usually cone-shaped (see Hubbell & Foster 1986). Tree-level scaling is important for some microclimate variables, such as PFD, which are affected more by smaller-scale components of forest structure than by stand-level processes (see Parker 1995). The fine-grain level at which changes in microclimate occur thus may result in niches in the vertical space under a canopy tree (Torquebiau 1988).

A second advantage of a tree-centered approach is that resulting data pertain to the microclimate environment experienced actually or potentially by tree leaves of a single species. There is little information available on the light environments utilised by individual tropical rain forest individual species (Oberbauer *et al.* 1988). Seedlings of the same species often share part of the same vertical profile as saplings or canopy trees. Further, leaves within the same canopy tree frequently occupy a range of heights, especially if the crown is deep. Leaves situated in different vertical positions are likely to be most affected by, and to affect, their immediate microclimate environment. Hence, an individual leaf's microclimate is often the product of the interception of light by adjacent leaves (see Caldwell *et al.*

1986); sub-canopy light environments are primarily the result of interception by leaves in the canopy (Ellsworth & Reich 1993) and upper trees will dominate the position of lower trees (Alexandre 1984). More particularly, light "filtered" by a maternal tree may effect the germination of its own seeds below (Orozco-Segovia *et al.* 1993).

In this study, I examine diurnal and, especially, spatial distributions of CO₂ concentration, temperature, relative humidity, vapour pressure deficit (VPD), and PFD. I compare the results with other vertical profile studies, and briefly identify trends which may be important in explaining leaf functioning in different forest height positions. Vertical and diurnal trends in leaf characteristics of the study tree are presented in another paper (Barker & Booth, in press). This study was not intended to be an exhaustive investigation of vertical microclimate in the forest. Discrepancies often exist between "near-leaf" and whole-canopy microclimate measurements (Fitzjarrald & Moore 1995), and no attempt is made here to scale-up measurements to canopy or forest as a whole. I conclude with some suggestions for further research.

Methods

Study site

The investigation was carried out in dipterocarp forest situated in the Bati Apoi Forest Reserve, Brunei (4° 31' N, 115° 08' E). The mean annual of rainfall in the area is approximately 4000 mm. The study site was located on a small, level spur on a steep valley side facing west. The forest is pristine, with no known history of large-scale disturbance by human activity (see Cranbook & Edwards 1994). Base rock of the area is shale, with a thin covering of clay.

The vertical microclimate profile was associated with a single *Dryobalanops lanceolata* Burck. ('kapur') tree, a common canopy tree of the area (Ashton 1964). The tree was 32.5 m high, with branches from 19 m above the ground and monopodial architecture. Diameter at breast height (DBH) of the tree was 36 cm. The tree was shaded to some extent by a single layer of loose upper canopy of an adjacent tree, ca. 10 m above. The forest canopy above was open to the west (i.e. facing away from the hillside) and mainly closed to the east. Access to the canopy was by ropes supported by the overhead tree.

Microclimate measurements

Sequential measurements were made of ambient CO₂, relative humidity (RH), photon flux density (PFD), and air temperature at 1-m intervals in a vertical transect approximately 30-50 cm from the tree bole, using a portable infra-red gas analyser (IRGA) (LCA3; Analytical Development Company, Hoddesdon, Herts., UK); technical specifications are given in Bingham & Long (1993). Measurements of microclimate using an IRGA have been reported in previous rain forest studies

(Yabuki & Aoki 1978, Kapos *et al.* 1993). PFD was measured by a selenium sensor mounted on the leaf cuvette (PLC; Analytical Development Company, Hoddesdon, Herts., UK) connected to the IRGA. The PFD sensor was in good agreement with that of a Li-Cor 6000 IRGA (Li-Cor Corp., Lincoln, NE, USA). Ambient air was pumped from the open leaf cuvette into the IRGA for analysis. CO₂ concentration was measured by the IRGA's infra-red sensor, calibrated daily using a standard CO₂ source. RH was determined by the IRGA's thin-film capacitance water vapor detector, recently factory-calibrated. Air temperature was measured by a thermistor in the leaf cuvette.

Daytime measurements were made during three 3-h or 2-h periods, distributed over three non-consecutive days in March 1992. The forest is essentially aseasonal, for example without substantial changes in forest structure due to leaf senescence. During two days which were generally cloudy (17 March) or clear (24 March), morning (0800-1100 h) and mid-day (1100-1400 h) measurements were made. Afternoon (1500-1700 h) readings were taken during another, mostly cloudy, day (22 March). Detailed information on the proportion of cloudy to clear days was not available, though from casual observations the great majority of days are cloudy or partly cloudy (P. Becker, pers. comm.). Sampling of forest microclimate during a total of a few hours or days is consistent with previous studies (e.g. Lemon *et al.* 1970, Aoki *et al.* 1978, Yoda 1978, Shuttleworth *et al.* 1985, Wofsy *et al.* 1988, Eliás *et al.* 1989), as is using a single sensor for a given variable at each height (Torquebiau 1988). Though more extensive sampling is desirable (Fitzjarrald & Moore 1995), as is simultaneous measurement at each sampling point, this was not possible here due to logistical constraints. Measurements commenced at the top of the canopy (33 m), and were made at 1-m intervals. Replicate (n = 2), spatially separated (ca. 1.5 m) measurements were made at each height during 17 March. Spatial variation was apparent, so during the subsequent sampling days (22, 24 March), replication was increased, and measurements were made in four compass directions (NESW) (n = 4), giving a vertical sampling 'cylinder', ca. 1.6 m in diameter. For all sampling days and each height, replicate measurements were averaged. Each replicate measurement was itself an average of stable readings obtained during each sampling (30 - 40 s). The total duration of sampling at each height was ca. 2.5 min. The time taken to complete one vertical transect (34 to 0 m) was ca. 1.5 - 2 h and it was assumed that differences in readings during this time were due to height rather than diurnal or climatic changes. Measurements during the duplicate days (17, 24 March) were out of phase, so that samples were obtained throughout each 3-h period. During any one vertical sampling, climatic conditions were fairly stable, and hence were not suspected of being a confounding factor. Atmospheric vapour pressure deficit (VPD) was calculated using RH and air temperature values. Although it is desirable to measure wind speed in microclimate studies (e.g. Aoki *et al.* 1978), equipment for this was not available in this study, though there was no appreciable sub-canopy wind during measurement periods, and in any case wind is not subject to much variation below the canopy (Kira & Yoda 1989). For each microclimate parameter, I tested for autocorrelations across the vertical profile, using SYSTAT™ (SYSTAT Inc., Evanston, IL, USA).

Results

Mean CO₂ concentrations were highest in the morning (mean = 375 ± 2 ppm) compared with mid-day and afternoon (means were 352 ± 2 and 349 ± 1 ppm respectively) (Figure 1). In general, CO₂ concentrations were similar on duplicate days. The variability of CO₂ concentrations was greatest in the morning (range = 107 ppm), and less during mid-day (range = 55 ppm) and afternoon (range = 28 ppm). Much of the change in CO₂ concentrations between diurnal periods occurred in the upper profile, particularly in the canopy region (> 25 m). Highest CO₂ concentrations (> 400 ppm) during morning and mid-day were mostly in the canopy region; the only exception was in the understory at 1 m during the morning of one day (mean = 409 ppm). Autocorrelations were apparent on one day, when CO₂ values for samples taken at heights 3 m apart were correlated (Table 1).

Table 1. Autocorrelation coefficients for microclimate variables measured in a vertical forest profile during three time periods. Only statistically-significant ($p \leq 0.05$) correlation coefficients (corr.) are shown. Lag values represent the "proximity" of autocorrelated data: lag = 1 refers to correlations between adjacent measurements, i.e. representing 1 m vertical distance. Lag = 2 and lag = 3 refer respectively to correlations between measurements separated by 2 m and 3 m heights. Standard errors for all these data were in the range 0.17 to 0.27.

Time period	Date	CO ₂		PFD		Temperature		RH		VPD	
		lag	corr.	lag	corr.	lag	corr.	lag	corr.	lag	corr.
0800 - 1100	17			1	0.594	1	0.672	1	0.560	1	0.707
	24	1	0.572	1	0.655	1	0.533	1	0.855	1	0.786
		3	0.549				2	0.734	2	0.608	
1100 - 1400	17					1	0.719	1	0.682	1	0.720
	24	1	0.482	1	0.673	1	0.670	1	0.474	1	0.567
		2	0.461								
1400 - 1700	22			1	0.655	1	0.871	1	0.905	1	0.906
						2	0.739	2	0.807	2	0.802

For the morning measurement period, PFD values were higher with increasing height in the canopy, with the mean above-canopy (> 32 m) value ($171.6 \pm 14.1 \text{ mol m}^{-2} \text{ s}^{-1}$) approximately three times greater than the lower understory (1-2 m) mean value ($58.0 \pm 3.0 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$) (Figure 1). Results for duplicate days were similar, despite one day being fairly cloudy and the other clear. 'Steeper' light gradients were measured between the above-canopy and lower understory during the mid-day and afternoon periods, probably due to the changing direction of incident PFD.

During the mid-day and afternoon periods the most rapid attenuation of PFD was at the canopy-atmosphere interface (ca. 32-34 m). Attenuations in PFD occurred from above-canopy (33-34 m) to top-canopy (31-32 m) by 45 % (morning), 70 % (mid-day), and 45 % (afternoon). Above-canopy to understory (1-2 m) reductions were respectively 65 %, 85 %, and 93 % for these periods. Above-

canopy PFD values were $691.2 \pm 175.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ at mid-day and afternoon values (22 March) were $797.6 \pm 1.8 \mu\text{mol m}^{-2} \text{s}^{-1}$. In the lower understory, the trend instead was far greater for morning ($102.7 \pm 4.7 \mu\text{mol m}^{-2} \text{s}^{-1}$), compared with afternoon ($58.3 \pm 4.8 \mu\text{mol m}^{-2} \text{s}^{-1}$) values. Relatively high PFD values at 22-24 m were apparent during the mid-day and afternoon periods, due either to an increase in lateral light or increased transmittance through the canopy. Autocorrelation between PFD readings occurred during each sampling day and (except 17 March, mid-day) measurement period (Table 1). Correlations occurred only between adjacent vertical sampling positions (lag = 1).

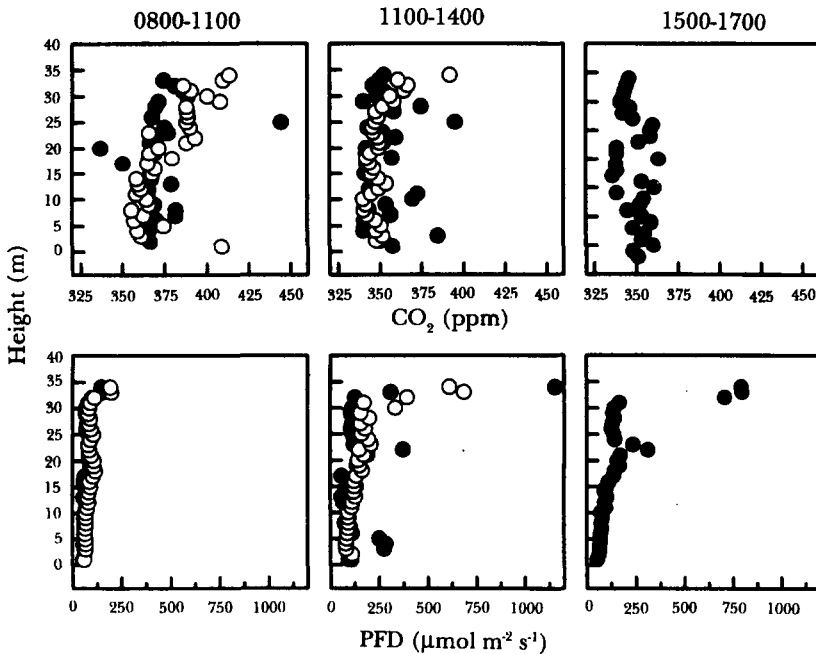


Figure 1. Carbon dioxide (CO₂) (top panel) and photon flux density (PFD) (lower panel) measured in a vertical forest profile during three time periods. Morning (0800-1100) and mid-day (1100-1400) measurements were made during a cloudy day (17 March; filled symbols) and a clear day (24 March; open symbols). Afternoon (1400-1700) measurements were made during a cloudy day (22 March; filled symbols). Each symbol is a mean of replicate readings made at each height: n = 2 (17 March) or n = 4 (22, 24 March).

Morning air temperature was fairly even (mean = $30.4 \pm 0.0 \text{ }^\circ\text{C}$) between 1 m and the top of the canopy (> 32 m), above which temperatures were up to 2 °C lower (Figure 2). Results for duplicate days were similar. Temperatures at all heights were ca. 3.5 °C higher by mid-day, and further increases (to ca. 34 °C) occurred at heights above 16 m by the afternoon. During the one day for which afternoon measurements were made, there was a marked gradient in temperature (2.4 °C) between 16 m and 17 m; this gradient was not apparent during previous measurement periods. Autocorrelations occurred between temperature measure-

ments for all days and measurement periods (Table 1). Correlations with lag = 1 indicate that adjacent (i.e. separated by 1 m) sampling positions were correlated. A lag = 2 for the afternoon period indicates that sampling points 2 m apart were also correlated.

Mean RH values for the whole profile were progressively lower from morning (mean = 60.3 ± 1.0) through mid-day (mean = 54.2 ± 0.5 %) to afternoon (mean = 51.9 ± 1.6 %) (Figure 2). Differences in vertical trends in RH were apparent between duplicate days. A negative gradient between RH and height occurred during the morning of the clearer day (22 March), but not during mid-day; the opposite trend occurred in the more cloudy day (17 March). For all times and days, there was a positive height-related gradient of RH from the upper canopy (29-31 m) to the atmosphere (> 32 m). A steep gradient (16.4 %) occurred in the vertical RH profile between 16 m and 17 m during the afternoon, congruent with that of temperature. Autocorrelation was apparent during all days and time periods, with correlation between samples 1 m apart (lag = 1) and 2 m apart (lag = 2) (Table 1).

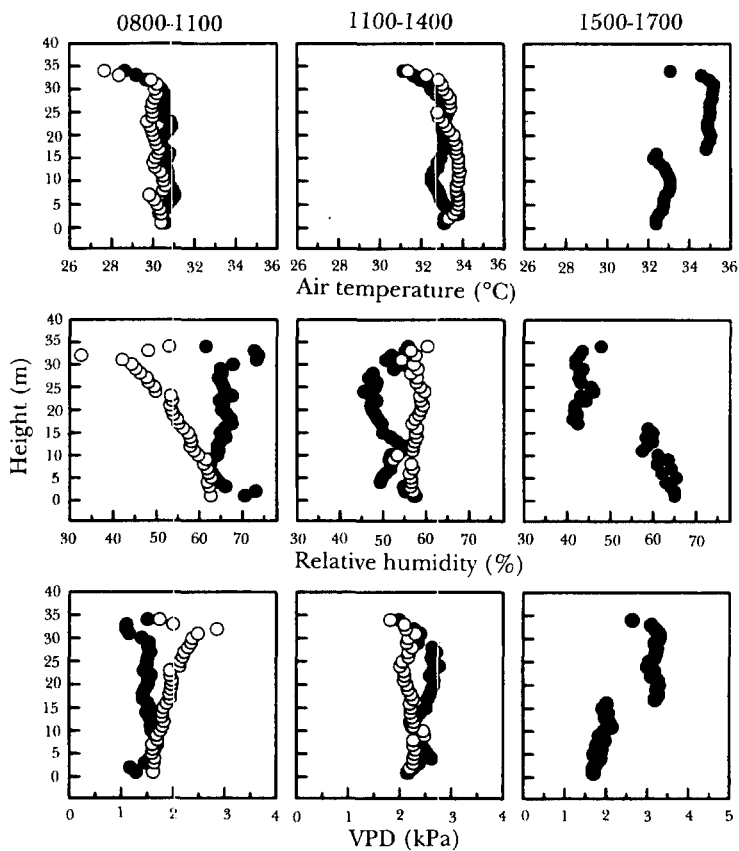


Figure 2. Air temperature (top panel), relative humidity (center panel) and vapor pressure deficit (VPD) (lower panel) measured in a vertical forest profile during three time periods. Sampling details are given in the caption for Figure 1.

Broad height- and time-related trends of VPD were a combination of air temperature and RH, of which VPD is a derivative (Figure 2). VPD was generally lowest for all heights during the morning (mean 1.71 ± 0.04 kPa), and during the more clear day (24 March), a gradient of increasing VPD with height was apparent; the range was 1.60 to 2.85 kPa. Gradients also occurred at the canopy/atmosphere interface, corresponding to those for temperature. There were progressive increases in mean VPD values for mid-day (mean = 2.32 ± 0.03 kPa) and afternoon (mean = 2.13 ± 0.11 kPa). A steep VPD gradient (1.18 kPa) between 16 m and 17 m for temperature (and, hence, VPD) was apparent on both measurement days. Auto correlation patterns for VPD conformed to those for temperature and RH (Table 1).

Discussion

Microclimate variables in the vertical profile associated with a canopy tree were heterogeneous, with distinct vertical gradients occurring for only some variables, particularly at the upper canopy/atmosphere interface. Broad diurnal shifts in the vertical distribution of CO₂ concentration, temperature, relative humidity, atmospheric VPD and PFD were apparent. During sampling periods for which there were replicate days (morning and mid-day), between-day variation was apparent for RH, and consequently also for VPD, but was much less apparent for other variables. Spatial autocorrelations have been used in few tropical forest microclimate studies (Baldocchi & Collineau 1994). Autocorrelations in this study showed that immediately adjacent samples (i.e. separated 1 m vertical distance) were usually not independent. Correlations with lags of 2 or 3 (i.e. separated respectively by 2 m or 3 m height) also occurred for the more "diffuse" parameters (CO₂, temperature, RH and VPD) but not for the more "discrete" parameter of PFD. This is consistent with a study of horizontal autocorrelation of light in seasonal tropical moist forest by Becker and Smith (1990), who found that light is correlated weakly at distances up to 2.5 m and not correlated beyond 5 m. More specific results for each microclimate variable are discussed below, with additional comments on possible leaf-microclimate relations.

My data support the observation (Bazzaz & Williams 1991) that seedlings, saplings and mature trees may experience different CO₂ environments. In general, results in this study are consistent with the contention by Björkman *et al.* (1972) that "there is no support to the old idea that air on rainforest floors is greatly enriched in CO₂ which would 'compensate' for low light levels in such habitats." The CO₂ concentration profiles in this study are not typical of the "inverted" gradients which have previously been reported in some temperate and tropical studies, with generally highest CO₂ concentrations near ground level (Medina & Minchin 1980, Kira & Yoda 1989, Bazzaz & Williams 1991). Soil respiration is normally a substantial source of CO₂ (Wofsy *et al.* 1988, Kira & Yoda 1989, Bazzaz & Williams 1991). In a Malaysian study, Kira & Yoda (1989) reported that ground surface CO₂ concentrations always exceeded 400 ppm. In this study, only on one day during the morning (at 1 m) did I record CO₂

concentrations > 400 ppm, comparable with results for a temperate forest (Eliás *et al.* 1989). The observed low CO₂ concentrations may have resulted from efficient turbulent movement and mass air flow (Baldocchi *et al.* 1986) in the fairly open sub-canopy. More likely, the relatively low quantity of litter, due to previous clearance of understory vegetation for a temporary camp, may have influenced the production of CO₂ from decomposition. Thus, this study provides very limited evidence to support the suggestion that understory leaves may be able to exploit high CO₂ concentrations during sunflecks (Mooney *et al.* 1984), but only up to about 1 m from the forest floor. In any case, the availability of CO₂ to understory leaves is a function of both concentration and transfer rate and, in the relatively still understory air, even high amounts of CO₂ may not be readily supplied to understory plants (Kira & Yoda 1989).

Diurnal changes in CO₂ concentration result from variations in wind speed (not determined in this study), solar radiation, air temperature, and also by gas exchange of vegetation associated with the profile (see Eliás *et al.* 1989). Reductions in CO₂ concentrations at mid-day are consistent with results of Kira and Yoda (1989), particularly for the canopy region, where assimilation rates are relatively high (Baldocchi *et al.* 1986, Kira & Yoda 1989). Comparable studies in a West Malaysian forest have revealed highest mid-day rates of CO₂ uptake at 10 m and at the canopy surface (30 - 40 m), with a negligible CO₂ gradient between 5 m and 53 m (Aoki *et al.* 1978, Kira & Yoda 1989). In the same profile as the present study, photosynthetic assimilation was greatest at ca. > 28 m during mid-day, and during the afternoon at 19 - 21 m (Barker & Booth, in press). Progressive diurnal upper-canopy (> 28 m) depletions of CO₂ probably resulted from higher morning and mid-day assimilation rates in this part of the profile.

Light was attenuated rapidly upon entering the canopy during the mid-day and afternoon periods; the most rapid reduction occurred within 1 m below the top of the canopy, a phenomenon observed in other forest studies (e.g. Caldwell *et al.* 1986, Eliás *et al.* 1989, Parker 1995). This was consistent with the 50 % through-canopy reduction in a vertical forest profile in West Malaysia (Aoki *et al.* 1978, Yoda 1978). Mean PFD throughout most of the study was < 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, consistent with a Costa Rican study (Oberbauer & Strain 1986). Mean understory (1-2 m) PFD values in the present study were in the range 7 - 35 % (overall mean, 15 %) of those above the canopy (33-34 m), with reductions increasing diurnally. PFD in tropical rain forest understories are typically given as ca. 1 % of above-canopy amounts (Chazdon & Fetcher 1984, Chiariello 1984, Kira & Yoda 1989) and higher values in this study may reflect the more open nature of this hillside site. Along with depletions in PFD from canopy to understory, there almost certainly was a change in light quality (e.g. as a reduction in red: far-red ratios, not measured in this study) which can affect plant photosynthesis and development (e.g. Orozco-Segovia *et al.* 1993). Photosynthetic gains in the study tree were highest in the upper surface of the canopy (31 m) in the morning and mid-day periods and highest in the mid-canopy (21 m) in the afternoon during two days immediately prior to the present study (Barker & Booth, in press). This is consistent with the proposition that increased amounts of light are admitted to the inner canopy

(Figure 1; see Ehleringer & Forseth 1989) when upper-canopy leaves become more erect after mid-day (pers. obs.). In the understory, the general lack of PFD gradients may mean that differences in initial height growth are not important for competition between seedlings (Grime & Jeffrey 1965).

Relatively high PFD in the mid-canopy, occurring during mid-day and afternoon at 22 - 23 m, corresponded with a space between layers of foliage (see Barker & Booth, in press). The additional light may have resulted from light scattering within this "empty" layer, a phenomenon referred to by Torquebiau (1988) as PFD "inversion." Another possible cause, since there was an apparent diurnal effect, was increased lateral light due to changing solar angle. Lateral light may be particularly important for sapling growth, and is not simply associated with sloping sites (Oberbauer *et al.* 1988). Relatively high mid-canopy PFD has been observed in other forest profiles (Torquebiau 1988, Eliás *et al.* 1989) and may provide an important opportunity for plants immediately below to grow into a vacant part of the profile (Torquebiau 1988).

There was little apparent influence of cloudy versus clear skies on the vertical profiles; in fact, mean above-canopy (> 32 m) PFD was greatest during mid-day of the more cloudy day, due to the maximum ($1156 \text{ mmol m}^{-2} \text{ s}^{-1}$) at 34 m. Other tropical rain forest studies have found that increased light transmission and also reduced attenuation often occurs through the canopy on cloudy days (Chazdon & Fetcher 1984, Baldocchi & Collineau 1994). General factors affecting PFD levels at any particular height in the canopy are the product of leaf area index (LAI), whilst diurnal shifts result from changes in the sun's position and in leaf inclination (e.g. see Caldwell *et al.* 1986, Baldocchi & Collineau 1994, Parker 1995). These causal factors have not been considered individually in this study, though LAI for similar forest in Malaysia is reported to be in the relatively high range of 5.5 to 6.0 (Kira & Yoda 1989), which would be expected to result in considerable light interception by the forest. The light compensation point, at least for seedlings, of *D. lanceolata* is ca. $39 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (M. Barker, unpub. data), a value that was always exceeded in the vertical profile; this suggests that net photosynthetic gains for leaves of this species could occur in any vertical position.

Air temperatures in the vertical profile were broadly similar to those in other tropical rain forests (Chiariello 1984, Shuttleworth *et al.* 1985), though distinct vertical gradients reported for some sites (Broadmeadow *et al.* 1992) were not observed here, or in a West Malaysian study (Kira & Yoda 1989). Consistent temperature gradients during the period 0800-1700 h were apparent only at the extreme limits at the canopy/atmosphere interface. It is likely that above-canopy depressions of ambient temperature (by about 2°C from the profile mean) resulted from increased air movement from wind and convection (Aoki *et al.* 1978, Kira and Yoda 1989). Relatively low understory temperatures may result primarily from low incidence of direct solar radiation. Results here are consistent with previous studies, showing a greater diurnal temperature range in the canopy compared with the understory (Mooney *et al.* 1984). Thus it is likely that leaves in the upper canopy are subjected to a higher heat load. This is offset in many canopy species (including

Dryobalanops lanceolata, pers. obs.) by upper-canopy leaves being more erect, or becoming so later in the day (pers. obs.).

The steep afternoon gradient in temperature, RH and, therefore, VPD between 16 m and 17 m is a conspicuous feature of the vertical profile. The possibility of instrument malfunction is unlikely because instrument function was normal before and after the 16 - 17 m transition. Also, a sharp drop in temperature could be felt when abseiling down the access rope in this region immediately below the canopy, and also in comparable situations in another dipterocarp forest in Brunei (pers. obs.). A second explanation for the mid-profile transition is an increase in lateral radiation (the site sloped to the west) which continued to raise temperatures above the shrub layer, whilst the more shaded understory layer became cooler. However, PFD increases were most apparent elsewhere in the profile (Figure 1), including at 22-23 m. It seems much more likely that the steep temperature gradient at 16 - 17 m may instead be an example of a wider phenomenon in tropical rain forests of a substantial decoupling of cooler, denser air beneath the canopy (i.e. < 19 m) in relation to lighter, warmer air above the canopy (see Shuttleworth *et al.* 1985, Dolman *et al.* 1991, Fitzjarrald & Moore 1995). There are indications of a dissociation in upper- and lower-profile RH during a comparable (i.e. cloudy) day during mid-day (Figure 2). The clear transition between canopy and sub-canopy temperatures, RH and VPD appears to provide direct evidence for an 'inversion surface', as described by Richards (1983) and Alexandre (1984).

Gradients of RH and VPD with height, observed during each period at least for part of the profile, have also been reported elsewhere (Aoki *et al.* 1975, Chiariello 1984, Broadmeadow *et al.* 1992). This study reveals complex variations in RH and VPD profiles both temporally (within and between days) and also in direction, similar to trends in an Amazonian study (Shuttleworth *et al.* 1985). VPD values were in broad agreement with those of other tropical rain forest studies (e.g. Grace *et al.* 1982, Oberbauer & Strain 1986, Broad meadow *et al.* 1992). RH tended to be lowest in the upper part of the profile, particularly in the afternoon, in common with Aoki *et al.* (1978). Both RH and VPD affect, and are affected by, leaves in the canopy. The higher afternoon VPD (about twice that of the morning) in the upper-canopy resulted from a combination of raised air temperature and lowered RH; this higher VPD would potentially increase leaf transpiration rates. However, to prevent excessive water loss canopy trees sometimes reduce afternoon transpiration rates, as was observed for the study tree in this study (Barker & Booth, in press). Conversely, transpiring leaves contribute to the RH of adjacent air (e.g. Shuttleworth *et al.* 1985), particularly during the early part of the day, when transpiration rates are typically high (e.g. Gallego *et al.* 1994). Differences in RH of up to 30 % can exist between canopy and understory positions (Chiariello 1984). In this study, mean understory (1 m) RH was always greater than that above the canopy, particularly in the afternoon.

In conclusion, my microclimate measurements provide evidence for both vertical and temporal variations in CO₂, air temperature, RH, VPD and PFD in the forest environment. Where gradients existed, they tended to correspond with abrupt vertical changes in the distribution of foliage, at the top of, and also beneath, the

main canopy. Results here confirm that profiles of different microclimate variables are not the same. Such differences in microclimate profiles are accounted for by their having differing sinks and sources (Parker 1995). The upper part of the profile, approximately corresponding to the tree crown, showed the greatest extent of diurnal variation for all parameters, in common with other studies (e.g. Shuttleworth *et al.* 1985).

The emphasis in this paper has been on describing the vertical microclimate as a milieu for leaf functioning. However, vertical gradients in microclimate have much broader implications. Tropical rain forests provide many niches in the vertical plane (Terbough 1985), and furthermore some plants can "forage" for available microsites below the canopy (Canham 1988, Castellanos *et al.* 1992). Species diversity in the vertical profile of tropical rain forests is high, though the reasons for this are not fully understood (Bourgeron 1983). Further studies are needed to characterise the distribution of vertical microsites. To provide more ecologically-robust information, the intensity and duration of microclimate sampling need to be increased in such studies (Kira & Yoda 1989). Above-ground horizontal profiles of both the forest structure (Koike & Syahbuddin 1993) and the physical environment, which are mutually dependent, have so far received little research attention. Thus, more comprehensive studies, including horizontal sampling, are needed, so that a better understanding of three-dimensional forest microclimate is obtained.

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References

- ARDHANA, I. P. G., TAKEDA, H., SAKIMOTO, M. & TSUTSUMI, T. 1988. The vertical foliage distributions of six understorey tree species in a *Chamaecyparis obtusa* Endl. forest. *Trees* 2 : 143 - 149.
- ALEXANDRE, D. Y. 1984. Strata in tropical rain-forest at Taï (Ivory Coast). Pp. 15 - 24 in Chadwick, A. C. & Sutton, S. L. (Eds.) *Tropical Rain-Forest: The Leeds Symposium*. Leeds Philosophical and Literary Society, Leeds, UK.
- AOKI, M., YABUKI, K. & KOYAMA, H. 1978. Micrometeorology of Pasoh forest. *Malayan Nature Journal* 30 : 149 - 159.
- ASHTON, P. S. 1964. Ecological studies in the mixed dipterocarp forests of Brunei state. *Oxford Forestry Memoirs* 25. 75 pp.
- BALDOCCHI, D. D., VERMA, D.R., MATT, D.R. & ANDERSON, D.E. 1986. Eddy correlation measurements of CO₂ efflux from the floor of a deciduous forest. *Journal of Applied Ecology* 23 : 967 - 976.
- BALDOCCHI, D. D. & COLLINEAU, S. 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. Pp. 21 - 71 in Caldwell, M. M. & Pearcy, R. W. *Exploitation of Environmental Heterogeneity by Plants*. Academic Press, San Diego, USA.
- BARKER, M. G. & BOOTH, W.E. Vertical profiles in a Brunei rain forest. II. Leaf characteristics of *Dryobalanops lanceolata* Burck. *Journal of Tropical Forest Science*. (In press).

- BARKER, M. G. & SUTTON, S.L. Low-tech methods for forest canopy access. *Biotropica* (In press).
- BAZZAZ, F. A. & WILLIAMS, W.E. 1991. Atmospheric CO₂ concentrations within a mixed forest: implications for seedling growth. *Ecology* 72 : 12 - 16.
- BECKER, P. & SMITH, A.P. 1990. Spatial autocorrelation of solar radiation in a tropical moist forest understory. *Agriculture and Forest Meteorology* 52 : 373 - 379.
- BENZING, D. H. 1995. The physical mosaic and plant variety in forest canopies. *Selbyana* 16 : 159 - 168.
- BINGHAM, M. J. & LONG, S.P. 1993. Equipment for plant physiology research in a changing environment. Pp. 357 - 421 in Hall, D. O., Scurlock, J. M. O., Bolh ar-Nordenkamp, H. R., Leegood, R. C. & Long, S. P. (Eds.) *Photosynthesis and Production in a Changing Environment*. Chapman & Hall, London, UK.
- BJ RKMAN, O., LUDLOW, M.M., MOROW, P. A. 1972. Photosynthetic performance of two rainforest species in their native habitat and analysis of their gas exchange. *Carnegie Institution of Washington Yearbook* 71: 94 - 102.
- BOURGERON, P. S. 1983. Spatial aspects of vegetation structure. Pp. 29-47 in Golley, F. B. (Ed.) *Ecosystems of the World: Tropical Rain Forest Ecosystems*. Vol. 14A. Elsevier, Amsterdam, Netherlands.
- BROADMEADOW, M. S. J., GRIFFITHS, H., MAXWELL, C. & BORLAND, A. M. 1992. The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO₂ within tropical forest formations in Trinidad. *Oecologia* 89 : 435 - 441.
- CALDWELL, M. M., MEISTER, H.-P., TENHUNEN, J. D. & LANGE, O. L. 1986. Canopy structure, light microclimate and leaf gas exchange of *Quercus coccifera* L. in a Portuguese macchia: measurements in different canopy layers and simulations with a canopy model. *Trees* 1: 25 - 41.
- CANHAM, C. D. 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69 : 786 - 795.
- CANHAM, C. D., DENSLOW, J.S., PLATT, W. J., RUNKLE, J. R., SPIES, T. A. & WHITE, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forestry Research* 20 : 620 - 631.
- CASTALLANOS, A. E., DUR N, R., GUZM N, S., BRIONES, O., FERIA, M. 1992. Three-dimensional space utilization of lianas: a methodology. *Biotropica* 24 : 396 - 401.
- CHAZDON, R. L. 1986. Light variation and carbon gain in rain forest understorey palms. *Journal of Ecology* 74 : 995 - 1012.
- CHAZDON, R. L. & FETCHER, N. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72 : 553 - 564.
- CHIARIELLO, N. 1984. Leaf energy balance in the wet lowland tropics. Pp. 85 - 98 in Medina, E., Mooney, H. A. & Vazquez-Yanes, C. (Eds.) *Physiological Ecology of Plants of the Wet Tropics*. Junk, Amsterdam, Netherlands.
- CRANBROOK, EARL OF, & EDWARDS, D. S. 1994. *Belalong: A Tropical Rainforest*. The Royal Geographical Society, London, UK.
- DOLMAN, A. J., GASH, J. H. C., ROBERTS, J. & SHUTTLEWORTH, W. J. 1991. Stomatal and surface conductance of tropical rainforest. *Agriculture and Forest Meteorology* 54 : 303 - 318.
- EHLERINGER, J. R. & FORSETH, I. N. 1989. Diurnal leaf movements and productivity in canopies. Pp. 129 - 142 in Russell, G., Marshall, B. & Jarvis, P. G. (Eds.) *Plant Canopies: Their Growth, Form and Function*. Cambridge University Press, Cambridge, UK.
- ELI S, P., KRATOCHV ILOV , I., JANOUŠ, D., MAREK, E. & MASAROVICHOV , E. 1989. Stand microclimate and physiological activity of tree leaves in an oak-hornbeam forest. *Trees* 4 : 227 - 233.
- ELLSWORTH, D. S. & REICH, P. B. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96 : 169 - 178.
- FIELD, C. B. 1988. On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. *Australian Journal of Plant Physiology* 15 : 343 - 358.
- FITZJARRALD, D. R. & MOORE, K. E. 1995. Physical mechanisms of heat and mass exchange between forests and the atmosphere. Pp. 45 - 72 in Lowman, M. D. & Nadkarni, N. M. (Eds.) *Forest Canopies*. Academic Press, San Diego, USA.
- GALLEGO, H. A., RICO, M., MORENO, G. & SANTA REGINA, I. 1994. Leaf water potential and stomatal conductance in *Quercus pyrenaica* Willd. forests: vertical gradients and response to environmental factors. *Tree Physiology* 14 : 1039 - 1047.

- GRACE, J. D., OKALI, U. U. & FASEHUN, F. E. 1982. Stomatal conductance of two tropical trees during the wet season in Nigeria. *Journal of Applied Ecology* 19 : 659 - 670.
- GRIME, J. P. & JEFFREY, D. W. 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* 53 : 621 - 642.
- HUBBELL, S. P. & FOSTER, R. B. 1986. Canopy gaps and the dynamics of a neotropical forest. Pp. 77 - 96 in Crawley, M. J. (Ed.) *Plant Ecology*. Blackwell, Cambridge, UK.
- KAPOUS, V., GANADE, G., MATSUI, E. & VICTORIA, R. L. 1993. $\delta^{13}\text{C}$ as an indicator of edge effects in tropical rainforest reserves. *Journal of Ecology* 81: 425 - 432.
- KIRA, T. & YODA, K. 1989. Vertical stratification in microclimate. Pp. 55-71 in Leith, H. & Werger, M. J. (Eds.) *Tropical Rain Forest Ecosystems*. Elsevier, Amsterdam, Netherlands.
- KOIKE, F. & SYAHBUDDIN. 1993. Canopy structure of a tropical rain forest and the nature of an unstratified upper layer. *Functional Ecology* 7 : 230 - 235.
- LEMON, E., ALLEN, L. H. & MULLER, L. 1970. Carbon dioxide exchange of a tropical rain forest. Part II. *BioScience* 20 : 1054 - 1059.
- LIEBERMAN, M., LIEBERMANN, D. & PERALTA, R. 1989. Forests are not just Swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70 : 550 - 552.
- MCWILLIAM, A.-L. C., ROBERTS, J. M., CABRAL, O. M. R., LEITO, M. V. B. R. de COSTA, A. C. L., MAITELLI, G. T. & ZAMPARONI, C. A. G. P. 1993. Leaf area index and above-ground biomass of *terra firme* rain forest and adjacent clearings in Amazonia. *Functional Ecology* 7 : 310 - 317.
- MEDINA, E. & MINCHIN, P. 1980. Stratification of $\delta^{13}\text{C}$ values of leaves in Amazonian rain forests. *Oecologia* 45 : 377 - 378.
- MOONEY, H. A., FIELD, C. & VAZQUEZ-YANES, C. 1984. Photosynthetic characteristics of wet tropical plants. Pp. 113 - 128 in Medina, E., Mooney, H. A. & Vazquez-Yanes, C. (Eds.) *Physiological Ecology of Plants of the Wet Tropics*. Junk, Amsterdam, Netherlands.
- OBERBAUER, S. F., CLARK, D. B., CLARK, D. A. & QUESADA, M. 1988. Crown light environments of saplings of two species of rain forest emergent trees. *Oecologia* 75 : 207 - 212.
- OBERBAUER, S. F. & STRAIN, B.R. 1986. Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra maculosa* (Mimosaceae). *American Journal of Botany* 73 : 409 - 416.
- OROZCO-SEGOVIA, A., SANCHEZ-CORONADO, M. E. & VAZQUEZ-YANES, C. 1993. Effect of maternal light environment on seed germination in *Piper auritum*. *Functional Ecology* 7 : 395 - 402.
- PARKER, G. G. 1995. Structure and microclimate of forest canopies. Pp. 73 - 106 in Lowman, M. D. & Nadkarni, N. M. (Eds.) *Forest Canopies*. Academic Press, San Diego, USA.
- RICHARDS, P. W. 1983. The three-dimensional structure of tropical rain forest. Pp. 3 - 10 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (Eds.) *Tropical Rain Forest: Ecology and Management*. Blackwell Scientific Publications, Oxford, UK.
- SHUTTLEWORTH, W. J. 1989. Micrometeorology of temperate and tropical forests. *Philosophical Transactions of the Royal Society* B 324 : 299 - 334.
- SHUTTLEWORTH, W. J., GASH, J. H. C., LLYOD, C. R., MOORE, C. J., ROBERTS, J., FILHO, A. de O. M., FISCH, G., FILHO, de P. S., RIBEIRO, M. de N. G., MOLION, L. C. B., de SA, L. D. A., NOBRE, J. C., CABRAL, O. M. R., PATEL, S. R. & de MORAES, J. C. 1985. Daily variation of temperature and humidity within and above Amazonian forest. *Weather* 40 : 102 - 108.
- SMITH, A. P., HOGAN, K. P. & IDOL, J.R. 1992. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* 24 : 503 - 511.
- TERBOUGH, J. 1985. The vertical component of plant species in temperate and tropical forests. *American Naturalist* 126 : 760 - 776.
- TORQUEBLAU, E. F. 1988. Photosynthetically active radiation environment, patch dynamics and architecture in a tropical rainforest in Sumatra. *Australian Journal of Plant Physiology* 15 : 327 - 342.
- WOFSY, S. C., HARRISS, R. C. & KAPLAN, W.A. 1988. Carbon dioxide in the atmosphere over the Amazon basin. *Journal of Geophysical Research* 93 : 1377 - 1387.
- YABUKI, K. & AOKI, M. 1978. Micrometeorological assessment of primary production rate of Pasoh forest. *Malayan Nature Journal* 30 : 281 - 289.
- YODA, K. 1978. Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Malayan Nature Journal* 30 : 161 - 177.