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THE INFLUENCE OF CLIMATIC CONDITIONS ON GAS AND ENERGY EXCHANGES ABOVE A YOUNG OIL PALM STAND IN NORTH KEDAH, MALAYSIA

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ABSTRACT

Measurements of fluxes of CO_2, latent heat and sensible heat were made above a three-year-old oil palm canopy in north Kedah, Malaysia where there is a regular dry season of three months or more annually. The results indicate substantially lower levels of CO_2 flux and latent heat flux (evapotranspiration) and substantially increased levels of sensible heat flux in the middle of the annual dry season in February, than in the succeeding wetter months of April to June. Canopy conductance for water vapour was likewise low during the drought and increased subsequently.

The use of these results as an aid to quantifying the responses of oil palm to water deficits is discussed.

Keywords: oil palm, eddy correlation, canopy photosynthesis, evapotranspiration, drought.

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INTRODUCTION

The land area in Malaysia occupied by oil palm has expanded to such an extent that land for further oil palm cultivation is increasingly difficult to obtain, especially in the Peninsula. One solution to this is to use areas generally regarded as unfit or marginal for oil palm in terms of resultant yield. Perhaps the most common limitation, other than altitude, topography and soils, is the seasonal distribution of rainfall.

In northern Kedah, while the total annual rainfall is adequate, there are at least three months each year (late December through to late March) when little or no rain falls and un-irrigated crops are dependent on soil reserves and ground water supplies. The possibility here, as for similar areas in southern Thailand, is to grow oil palm with irrigation. In view of this, MPOB has established a trial in a plantation near Sintok (6.27º N, 100.29º E) to assess the yield responses to irrigation and to relate these to the impact of drought on the physiology and growth of the palms.

Micrometeorology offers one approach to assessing the responses of vegetation to the environment. In this article, we present some initial results of micrometeorological measurements of energy and gaseous fluxes above an oil palm canopy with the view to examining the impact on these fluxes, of changes in climatic conditions. We used an eddy correlation or covariance (EC) technique which is one of the most sensitive and useful methods for assessing gas exchange of the whole canopy. With micrometeorological methods, no enclosure of the canopy is required and hence, there is minimal disturbance to the natural environment. In principle, an EC system can be operated 24 hr a day and allows continuous, largely unattended, readings to be made over long periods.

Of the micrometeorological methods that have been used in crop studies, the EC technique is increasingly employed due to its relative ease of operation compared to alternative methods, facilitated by the commercial development of improved *in situ* open path gas analysers, sonic anemometers and data logging systems. Unlike other methods, EC directly measures the turbulent fluxes rather than calculating them based on gradient measurements. The EC technique is thus tending to replace the older, indirect and more cumbersome Bowen ratio and aerodynamic methods. For

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information on the principles of the method, the reader is referred to standard texts such as Monteith and Unsworth (1990). Also, Tanner (1988) provides a brief yet lucid overview of the EC method.

This article reports and contrasts the results of measurements made under dry season conditions in February 2004 and during the succeeding wet months.

MATERIALS AND METHODS

Site and Crop

Details of the site, its climate and plot layout are described by Henson *et al*. (2005). The soil is a sandy clay loam of Batu Lapan series (Plinthic Hapludult, USDA classification) with a calculated available water holding capacity in the top 1 m of about 110 mm. The area planted to oil palm also extended into a zone with lateritic soil some 300 m to the south of the trial site.

Part of the trial area was provided with a drip irrigation system, though this was not operating during the time of our measurements. The measuring equipment was located outside the irrigated area.

The oil palm was planted in July 2000 at a density of 148 ha^{-1} in association with a leguminous cover crop.

Standard non-destructive measurements (Corley *et al*., 1971) were made at six-month intervals to determine the standing biomass and above-ground vegetative dry matter production. Age-dependent corrections were applied to the leaf area and dry matter data as described by Henson (1993). Root growth was assessed annually from auger samples with turnover being deduced by the in-growth core method (Henson and Chai, 1997). Fruit bunch numbers and fresh weights were recorded at each harvest and bunch dry matter was calculated as 53% of the fresh weight (Corley *et al*., 1971).

At the time of measurements (between February and June 2004), the palm canopy had a radius of 3.5 to 3.7 m (as measured in December 2003 and again in June 2004), a leaf area index based on total ground area of 1.6 to 2.0, and covered, on average, about 60% of the ground area. The leguminous cover crop and native vegetation had largely died back early in the dry period preceding the EC measurements.

Equipment

Instruments for EC measurements were installed on or close to an 8.7 m tall scaffolding tower (*Figure 1*). The tower was located so as to maximize the upwind fetch (distance from the edge of the planting to the measuring site). In terms of the measured stand, this was around 220 to 270 m depending on wind direction. Further oil palm of similar age was present outside of the southern limit, while there was an extensive, though younger planting, to the north.

The installed instruments and their uses are listed in *Table 1*. The flux measurements were made using

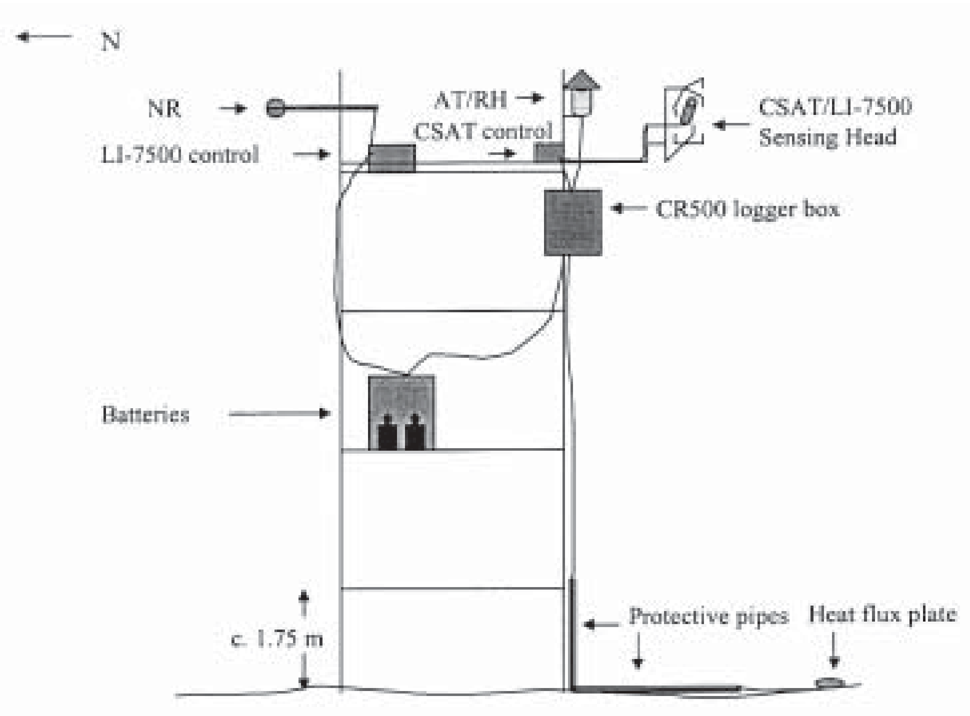

Figure 1. Location of eddy correlation and related instruments on the supporting tower (not to scale). Key: NR, net radiometer; AT, air temperature sensor; RH, relative humidity sensor. Other instruments are designated by manufacturer's model number (see Table 1 *for details).*

a sonic anemometer in combination with an open path CO_2/H_2O analyser. Additional instruments were installed to assist interpretation of the measured fluxes. These comprised a net radiometer, air temperature and relative humidity probes and soil heat flux plates. The outputs from these sensors were recorded and the fluxes were calculated *on-line* using a dedicated datalogger-cum-processor (Campbell Scientific Inc CR5000 measurement and control system). Power to the instruments was provided from two 12 V/150 amp-hour deep cycle batteries charged by three 75 W crystalline solar panels.

The sonic anemometer and open path gas analyser were mounted above the centre of a palm crown, 7 m above the ground and about 1 m above the mean canopy top.

Other meteorological instruments were mounted on two other similar towers within 30-40 m of the EC equipment (Henson *et al*., 2005). These served as either back-ups to confirm the EC site readings or to provide additional sensor measurements. They included sensors for air temperature, humidity, wind speed, rainfall, solar radiation, net radiation, photosynthetically active radiation (PAR) and canopy temperature. They are also listed in *Table 1*.

Soil water content was monitored fortnightly using a Delta-T Profile Probe (PR1, Delta-T Devices, Ltd, Burwell, United Kingdom) inserted into plastic access tubes installed in the experimental plots. The instrument measures volumetric water content by sensing changes in the dielectric constant. One group of 10 access tubes was close to the EC support tower. The measurements were made manually, but for one

TABLE 1. MICROMETEOROLOGICAL MONITORING EQUIPMENT USED IN THE STUDY

Sensor	Variable(s) measured	Units of measurement	Model	Manufacturer/ supplier
Sonic anemometer	Three-dimensional wind speed	$m\ s^{-1}$	CSAT3	Campbell Scientific Inc., Logan, UT, USA
Infrared gas analyser	CO_2 and H_2O concentrations	$mg\ m^{-3}$ and $g\ m^{-3}$	LI-7500	Licor Biosciences, Lincoln, NE, USA
Net radiometer	Net radiation	$W\ m^{-2}$	Q-7.1	Campbell Scientific Inc., Logan, UT, USA
Platinum resistance temperature and capacitive humidity sensors	Air temperature and relative humidity	°C and %	CS500	
Thermopile	Soil heat flux	$W\ m^{-2}$	HFT3	
Thermistor	Air temperature	°C	SKH 2013	Skye Instruments Ltd., Llandrindod Wells, UK
Temperature/RH capacitance sensor	Air temperature/ relative humidity	°C/%	Hobo H8	Onset Computer Corp., MA, USA
Cup anemometer	Horizontal wind speed	$m\ s^{-1}$	AN1	Delta-T Devices Ltd., Burwell, UK
Rain gauge	Rainfall	mm	RG1	
Infrared thermocouple	Canopy surface temperature	°C	Irt/c	Exergen, Watertown, MA, USA
Silicon energy sensor	Solar radiation	$W\ m^{-2}$	SKE 510	Skye Instruments Ltd., Llandrindod Wells, UK
Quantum sensor	Photosynthetically active radiation	$\mu mol\ m^{-2}\ s^{-1}$	SKP 215	

tube location from mid February onwards, a measuring probe was permanently installed in an access tube and its output logged hourly. Data were recorded at 100, 200, 300, 400, 600 and 1000 mm depths. Available soil water content (ASWC) was calculated as the soil water held in the top 1000 mm between tensions of –0.033 to –1.5 MPa.

Data Collection and Analysis

All data were automatically logged and stored as hourly means or totals, based on a sampling frequency of 10 s for conventional instruments and 100 m s (10 Hz) for flux data.

The logger was programmed to calculate the hourly fluxes of CO_2 (mg m^{-2} s^{-1}), momentum (kg m^{-1} s^{-2}), latent and sensible heat (W m^{-2}). It also provided data on mean horizontal wind speed (m s^{-1}) and direction. Further parameters were derived from these data including actual evapotranspiration (AET), available energy (AE), Bowen ratio (β), atmospheric vapour pressure deficit (VPD) and aerodynamic and canopy conductances (g_a and g_c) (see the *Appendix* for details). Potential evapotranspiration (PET) was calculated from the instrument readings using the form of the Penman equation adopted by Jensen *et al.* (1993).

During flux measurements, sustained rainfall events generally resulted in water droplets interfering with measurements by the sonic anemometer and open path gas analyser. During such times, it was not possible to obtain reliable CO_2, energy or momentum fluxes and consequently the data had to be screened to exclude such aberrant results from further analysis.

Corrections were required to the raw fluxes of latent heat (water vapour) and CO_2 as described by Webb *et al*. (1980) and Leuning *et al*. (1982). These were applied to the collected data. They take into account the effects on the *in situ* fluxes of the simultaneous transfer of sensible and latent heat. The effect of the corrections was to increase slightly the water vapour flux while reducing that of CO_2.

It should be noted that in presenting results in this paper, the sign convention for the CO_2 flux has been reversed (*i.e.* downward fluxes are treated as positive). This is to aid comparison with changes in radiation and vapour pressure deficit and to emphasize that a downward flux represents an addition of carbon to the ecosystem.

RESULTS AND DISCUSSION

Measurements commenced during the middle of the 2004 dry season in mid February. Little rain had fallen since mid December 2003 (*Figure 2*). Programming problems interrupted measurements in March when the rains resumed, precluding observations during the immediate rewetting of the soil profile. Further measurements were carried out from April onwards. Even though April was a wet month, most of the rain fell at the end of the month and it was, therefore, intermediate between the dry period in February and the following wet months in terms of soil water reserves, due to incomplete refilling of the profile.

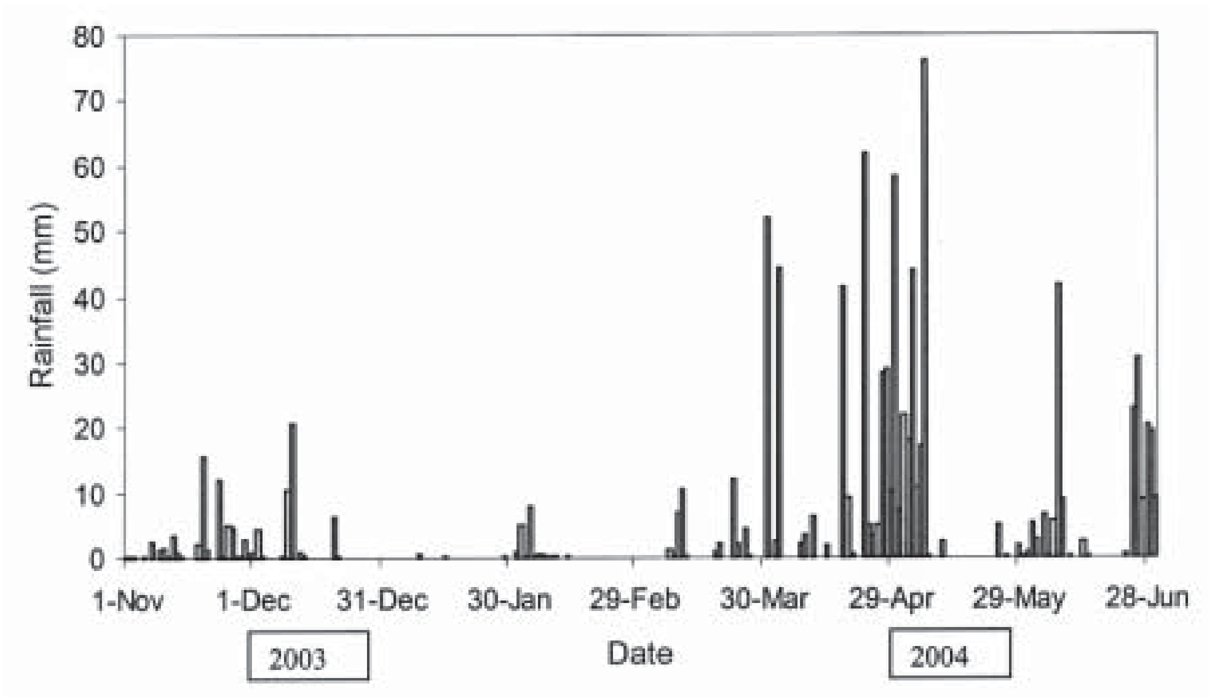

Figure 2. Daily rainfall at the experimental site from November 2003 to June 2004.

Climatic and Environmental Conditions

Meteorological data are presented in *Table 2*, while the detailed rainfall pattern spanning the period of the measurements is shown in *Figure 2*. Only 17 mm of rain were recorded at the site during the whole of February and less than 1 mm fell during the measurement period, vastly below the PET requirement, while the total monthly rainfalls during April to June exceeded evaporative requirements (*Table 2*).

Marked diurnal cycles occurred in the concentration of CO_2 detected above the canopy (*Figure 3*). There was a regular overnight build up of CO_2, presumed to represent efflux from the canopy and ground, as a consequence of plant and microbial respiration. This would have been facilitated by the lower wind speeds common during the night (Henson and Mohd Haniff, 2005). As shown in *Table 4*, the concentrations attained were quite substantial (>600 µmol mol^{-1}). The daily minimum values were lower and the maximum values of CO_2 concentration higher, in the wet than in the dry season. The lower minimum values can be related to the higher rates of photosynthesis recorded in the wet season, while the higher maxima can be accounted for by a combination of lower wind speed and, perhaps, higher respiratory activity during those months.

TABLE 2. CLIMATIC AND ENVIRONMENTAL CONDITIONS DURING DRY (February) AND WET (April-June) MONTHS IN 2004*

Month	Rain mm	ASWC %	AT °C	U m s^{-1}	VDP kPa	Solar radiation MJ m^{-2} day^{-1}	AE W m^{-2}	PET mm day^{-1}
February	0.4	75.4	26.97	2.01	1.93	19.57	232	4.28
April	313.8	84.7	27.38	1.21	0.98	18.09	294	4.44
May	207.2	96.3	27.06	1.18	1.19	17.16	269	3.92
June	187.0	95.9	26.54	1.47	1.07	15.72	237	3.80

Notes: *For February, the data cover the last 16 days only from when EC measurements started. For other months, the data refer to the whole month. ASWC (available soil water content) data refer to the mid-point of each period. Air temperature (AT; 24 hr mean), daytime wind speed (U); daytime vapour pressure deficit (VPD) and daytime available energy [AE = net radiation (Rn) – ground heat flux (G)] are daily means of hourly records. PET is the potential evapotranspiration rate.

Wind speeds and VPD were highest in February and lower in April and May, while PET and AE were both highest in April (*Table 2*). The higher air temperatures in April may have partly accounted for this. Mean wind speeds calculated from sonic anemometer data closely matched those from cup anemometers except at low speeds when the latter become insensitive.

There were sharp contrasts in the ASWC. ASWC was lowest in February and increased during April. By May, as a result of the foregoing rains, the profile had almost attained its maximum water holding capacity.

Wind direction differed markedly between months, being highly consistent in February but variable in April and May. Average wind direction and the corresponding fetch are given in *Table 3*. Wind direction did not differ appreciably between day and night.

TABLE 3. WIND DIRECTION AND ESTIMATED FETCH DURING THE MEASUREMENT PERIODS

Month	Wind direction (°)			Fetch (m)
	Day	Night	Mean	(approximate)
February	41	49	45	220
April	187	158	173	270
May	226	210	219	270
June	228	202	215	270

Concentrations of water vapour (absolute humidity) were also higher in the wet season (*Table 4; Figure 3*).

That the build up of CO_2 above, and presumably also within, the canopy, was related to wind speed and hence to momentum flux, is supported by the seasonal differences in aerodynamic conductance (g_a) (*Table 4*). The g_a was substantially higher in February in agreement with the higher mean wind speed (*Table 2*).

Responses

Overview of gas and energy fluxes. *Table 5* shows the mean values of daylight fluxes, surface conductance and other variables including the mean daily totals of AET and the AET/PET ratio for the dry and wet months.

Rates of daytime CO_2 uptake (given as mean hourly values where a downward flux represents uptake) and surface conductance were very low during the dry month of February but had increased substantially by April (*Table 5*). Related to the surface conductance, there was a decrease, from a high value

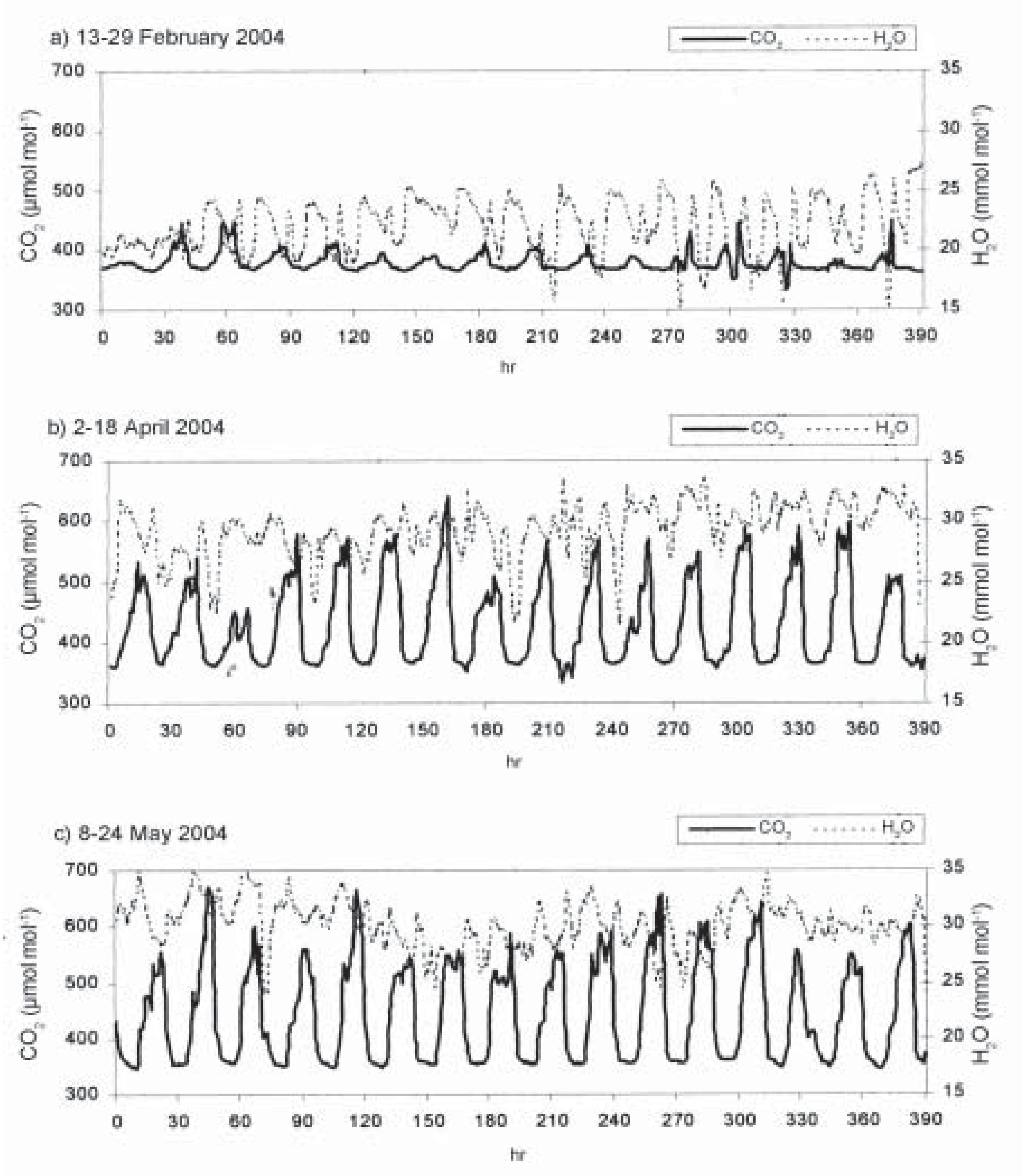

Figure 3. Changes in CO_2 and H_2O concentrations above the canopy over 16-day periods in dry (February) and wet (April, May) months.

TABLE 4. MINIMUM, MAXIMUM AND MEAN CO_2 AND H_2O CONCENTRATIONS ABOVE THE CANOPY AND DAY AND NIGHT-TIME AERODYNAMIC CONDUCTANCE (g_a)

Month	$[CO_2]$ (µmol mol^{-1})			$[H_2O]$ (mmol mol^{-1})			g_a (mm s^{-1})	
	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Day	Night
February	362	378	450	13.10	22.05	27.00	70.12	30.02
April	326	425	639	15.53	29.07	44.26	35.17	18.05
May	326	433	670	17.35	29.66	47.11	32.98	15.02
June	340	438	716	24.50	29.62	37.20	38.00	13.03

TABLE 5. STAND RESPONSES IN TERMS OF MEAN HOURLY DAYTIME CO_2, LATENT HEAT (LE) AND SENSIBLE HEAT (H) FLUX, BOWEN RATIO (β), SURFACE (canopy) CONDUCTANCE (g_C), CANOPY-AIR TEMPERATURE DIFFERENCE (ΔT), DAILY ACTUAL EVAPOTRANSPIRATION (AET) AND DAILY ACTUAL/POTENTIAL EVAPOTRANSPIRATION (AET/PET)*

Month	CO_2 uptake	LE	H	β	g_c	ΔT	AET	AET/PET
	$g\ m^{-2}\ hr^{-1}$	$W\ m^{-2}$	$W\ m^{-2}$		$mm\ s^{-1}$	°C	$mm\ day^{-1}$	
February	0.54	63.2	163.6	2.60	1.18	2.59	1.27	0.297
April	1.59	198.6	70.1	0.35	6.90	0.41	3.60	0.811
May	1.92	190.1	50.1	0.26	10.63	0.23	3.52	0.898
June	1.91	149.5	44.5	0.30	7.07	0.30	3.32	0.874

Notes: *CO_2 uptake, β and g_c were corrected for LE and H flux, and LE was corrected for H. Daytime was defined as all hours with a mean solar radiation >5 W m^{-2}. Data exclude times with aberrant flux readings due to rain.

in February, in the mean canopy to air temperature difference (ΔT), consistent with higher transpiration rates and evaporative cooling of leaf surfaces.

There was a particularly substantial impact of season on the fluxes of sensible (H) and latent heat (LE), and hence, on the rate of evapotranspiration. In February, H was the dominant component of the energy balance but this was reversed in April, May and June resulting in values of the daytime β falling from a high of 2.6 in February to below unity in the wet months (*Table 5; Figure 4*). In February, mean daytime hourly values of LE were only around 32% of those in April.

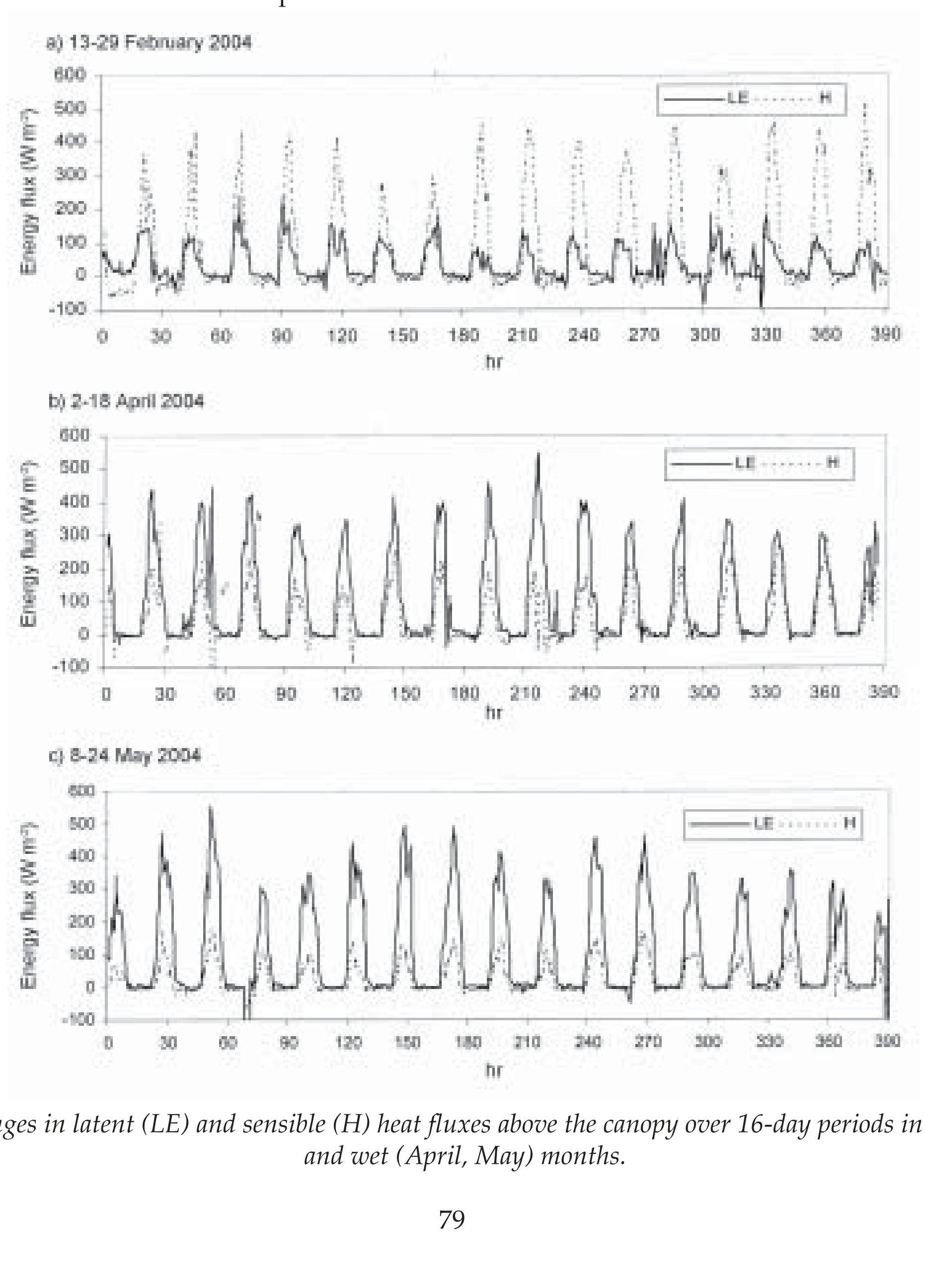

Figure 4. Changes in latent (LE) and sensible (H) heat fluxes above the canopy over 16-day periods in dry (February) and wet (April, May) months.

The sum of H and LE represents the available energy (AE) for heat transport. A test of the system performance is possible by comparing AE calculated as H + LE (*Table 5*) with AE calculated as Rn–G (*Table 2*) where Rn is the net radiation and G is the ground heat flux.

H + LE was 97.8% of AE calculated as Rn-G in February, indicating good agreement between the two independently derived sets of values. The equivalent figures for April, May and June were 91.5%, 89.3% and 82.3%. The poorer agreement during the latter months can be partly explained by the data loss due to rainy periods and the loss of one of the heat flux plates necessitating the use of regression equations to compensate for the missing values.

The daily evapotranspiration rate (actual ET or AET, to distinguish it from the potential ET or PET), calculated from LE and the latent heat of vaporization, was only 30% of PET during February, but had increased to nearly 90% by May.

The increase in AET was also reflected in changes in canopy conductance to water vapour (g_c), which increased dramatically in April, with a further rise in May, in line with the higher CO_2 uptake and AET/PET (*Table 5*).

It should be borne in mind that AET and g_c include a component of direct evaporation of free water such as that arising from rainfall and condensation on plant and soil surfaces. Interception of rainfall by the canopy was calculated using a simple model based on the canopy leaf area index (LAI). Details are given in the *Appendix*. Depending on the amount and distribution of rainfall, the interception in the wet months ranged from 9.9% to 18.1% of total AET (*Table 6*).

TABLE 6. ESTIMATED INTERCEPTION OF RAINFALL (daily mean) BY THE CANOPY AND INTERCEPTION AS A % OF DAILY ACTUAL EVAPOTRANSPIRATION (AET)

Month	AET	Intercepted rainfall	
	mm	mm	% of AET
February	1.27	0	0
April	3.60	0.54	15.0
May	3.52	0.35	9.9
June	3.32	0.60	18.1

CO_2 fluxes. Examples of hourly changes in CO_2 flux over 16-day continuous periods (selected as far as possible to avoid rain days) are shown in *Figure 5*. The very marked seasonal differences in the magnitude of CO_2 downward flux during the day are exemplified by these results. The daily peaks in CO_2 flux during February were generally below 1 g m^{-2} hr^{-1} while in April they approached or exceeded two and in May were two or above.

It is noticeable in all three periods that the peaks in CO_2 flux did not coincide with those in solar radiation. This is more clearly seen in *Figure 6* which shows data for only five-day periods, again for the three contrasting months. CO_2 flux peaked early in the morning and then generally declined thereafter, quite sharply in the driest month of February but more gradually in April. For the days shown in May, this is less evident. The difference can be accounted for by the lower VPD levels prevailing in the May examples compared with the preceding ones. This pattern confirms previous results (Henson, 1991a; 1995), whereby both the rates of leaflet photosynthesis and canopy CO_2 assimilation decline with an increase in VPD, which is most marked during the later part of the day. The generally maximum assimilation rates quite early in the morning probably also reflect the high initial CO_2 concentrations (*Figure 3*) as well as the low VPD at that time.

Correlations between variables. The relationship between variables was further explored using correlation analysis. CO_2 uptake by the canopy showed a curvilinear response to solar radiation (*Figure 7*) with little additional increase above about 500 W m^{-2} even in the wet months. There was even evidence of a slight decline in April and May above 600 W m^{-2} while in February, the flux peaked at an even lower level of radiation at around 500 W m^{-2}.

The declines in CO_2 flux at high radiation levels were most likely a result of the higher VPD at high radiation. There is now abundant evidence that VPD exerts a major influence on canopy photosynthesis via its effect on stomatal conductance (Smith, 1989; Dufrene, 1989; Henson, 1991a; 1995; Setyo *et al.*, 1996).

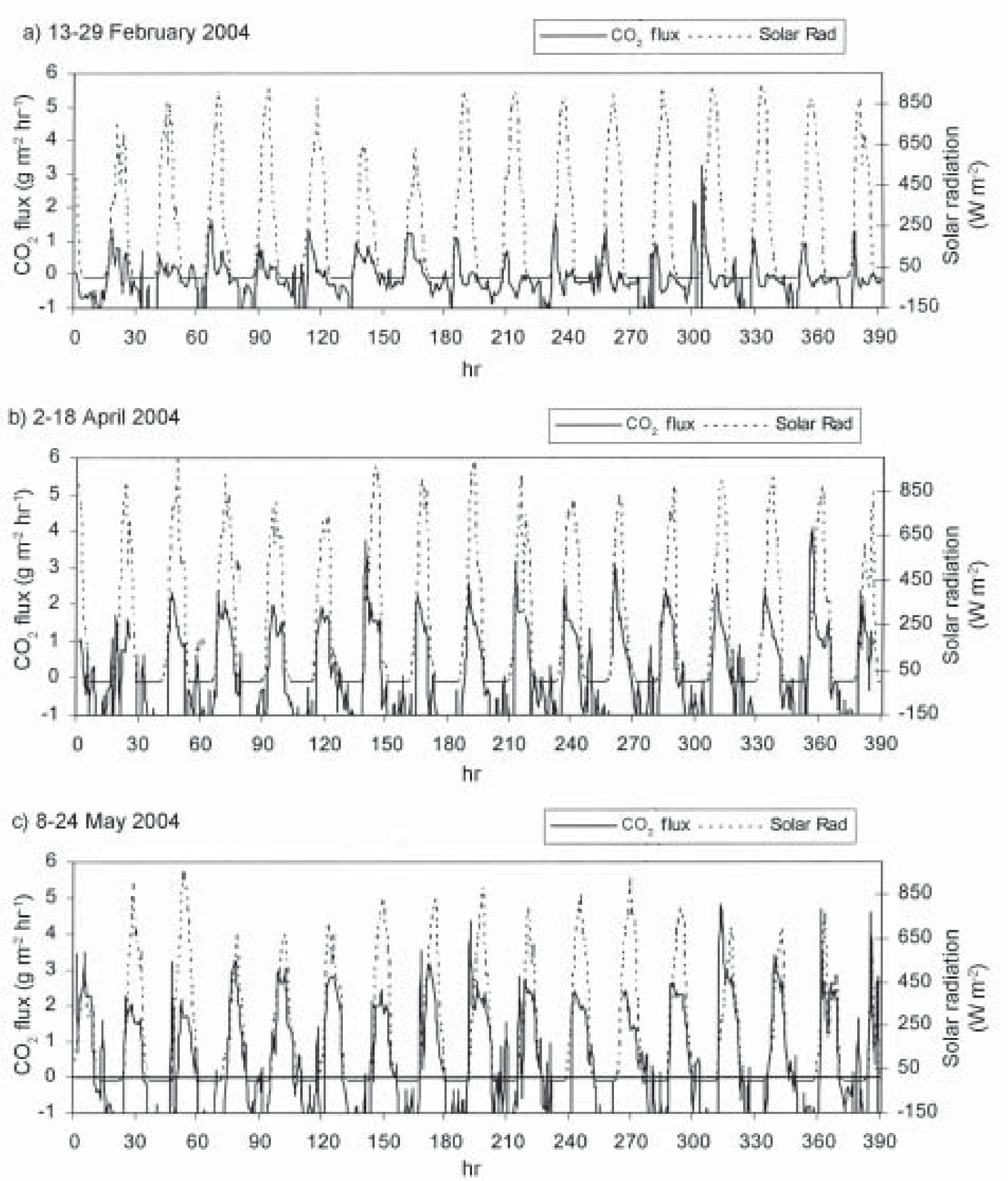

Figure 5. Changes in above-canopy CO_2 flux and solar radiation over 16-day periods in dry (February) and wet (April, May) months. Note that the direction of flux presented here is the reverse of the normal convention whereby flux to the surface (representing uptake) is negative.

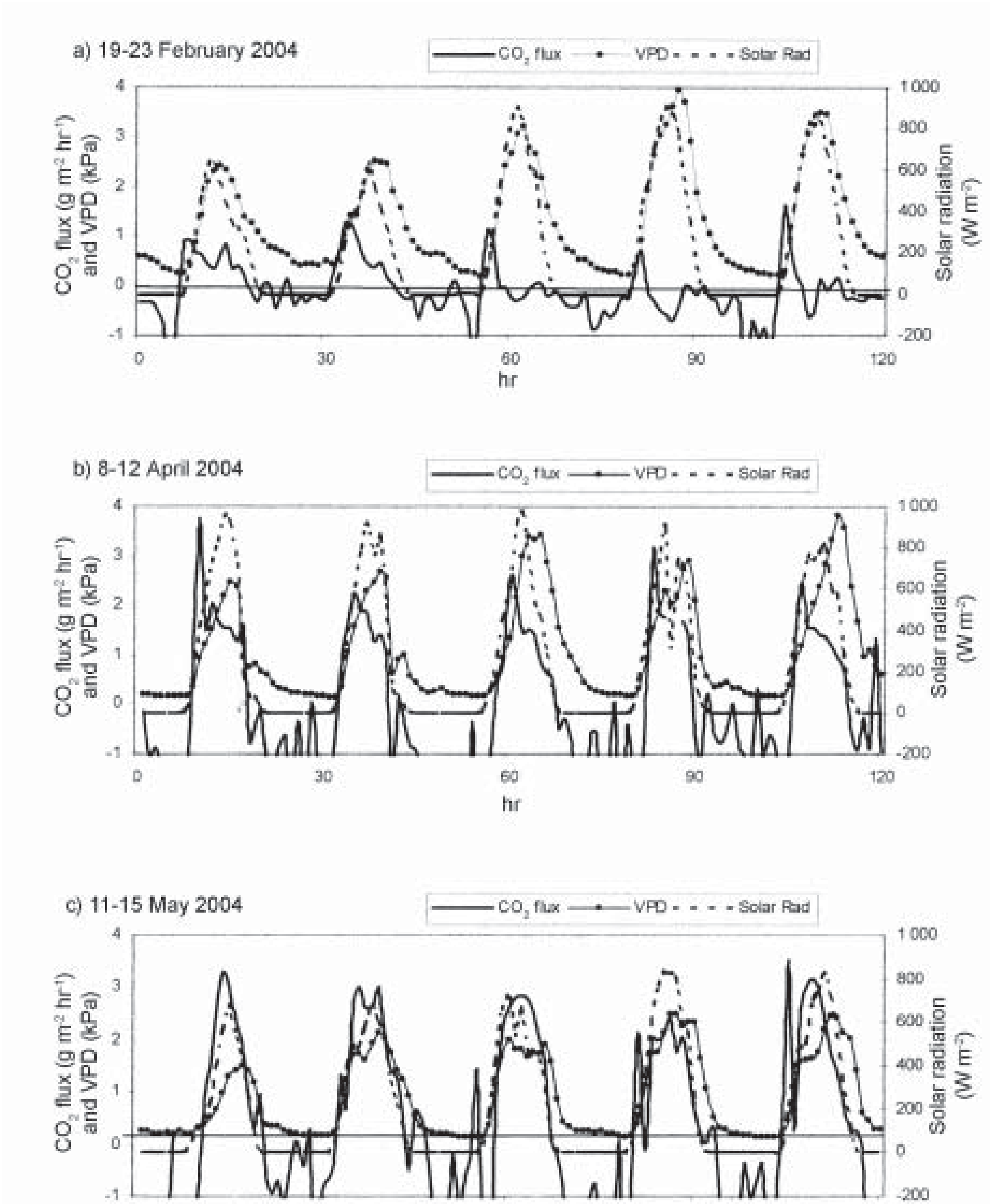

Figure 6. Examples of diurnal changes in CO_2 flux, solar radiation and atmospheric vapour pressure deficit (VPD) above the canopy over five-day periods in dry and wet months. To facilitate comparisons, all graphs are plotted on the same vertical and horizontal scales.

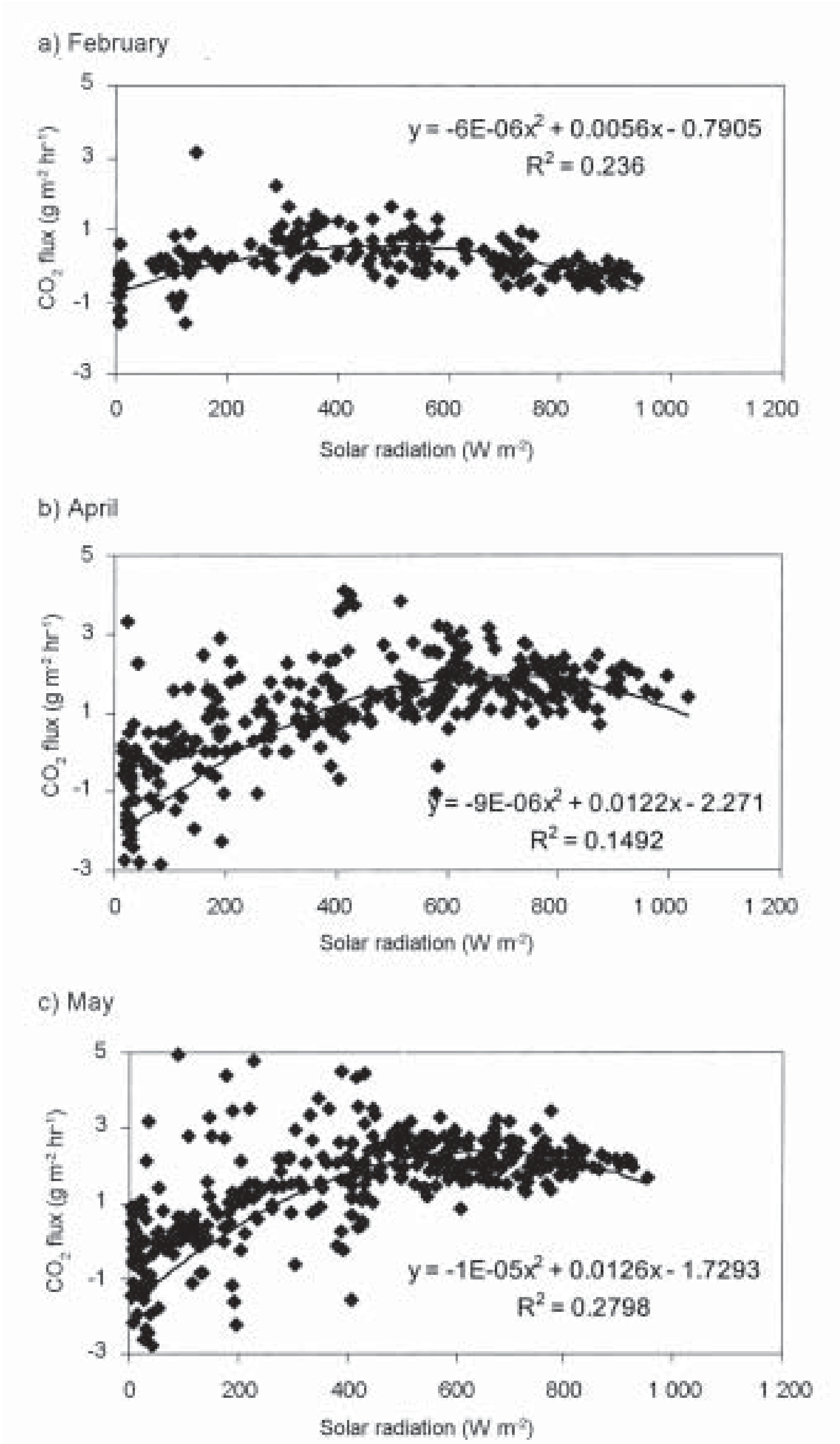

Figure 7. Relationships between hourly CO_2 flux above the canopy and incident solar radiation in dry (February) and wet (April, May) months. To facilitate comparisons, all graphs are plotted on the same vertical and horizontal scales.

Canopy CO_2 uptake data for radiation levels >700 W m^{-2} were hence plotted against VPD (*Figure 8*). The relationship was, as expected, negative, with similar slopes in all months though with the most significant and steepest decline being in the dry month of February (*Table 7*).

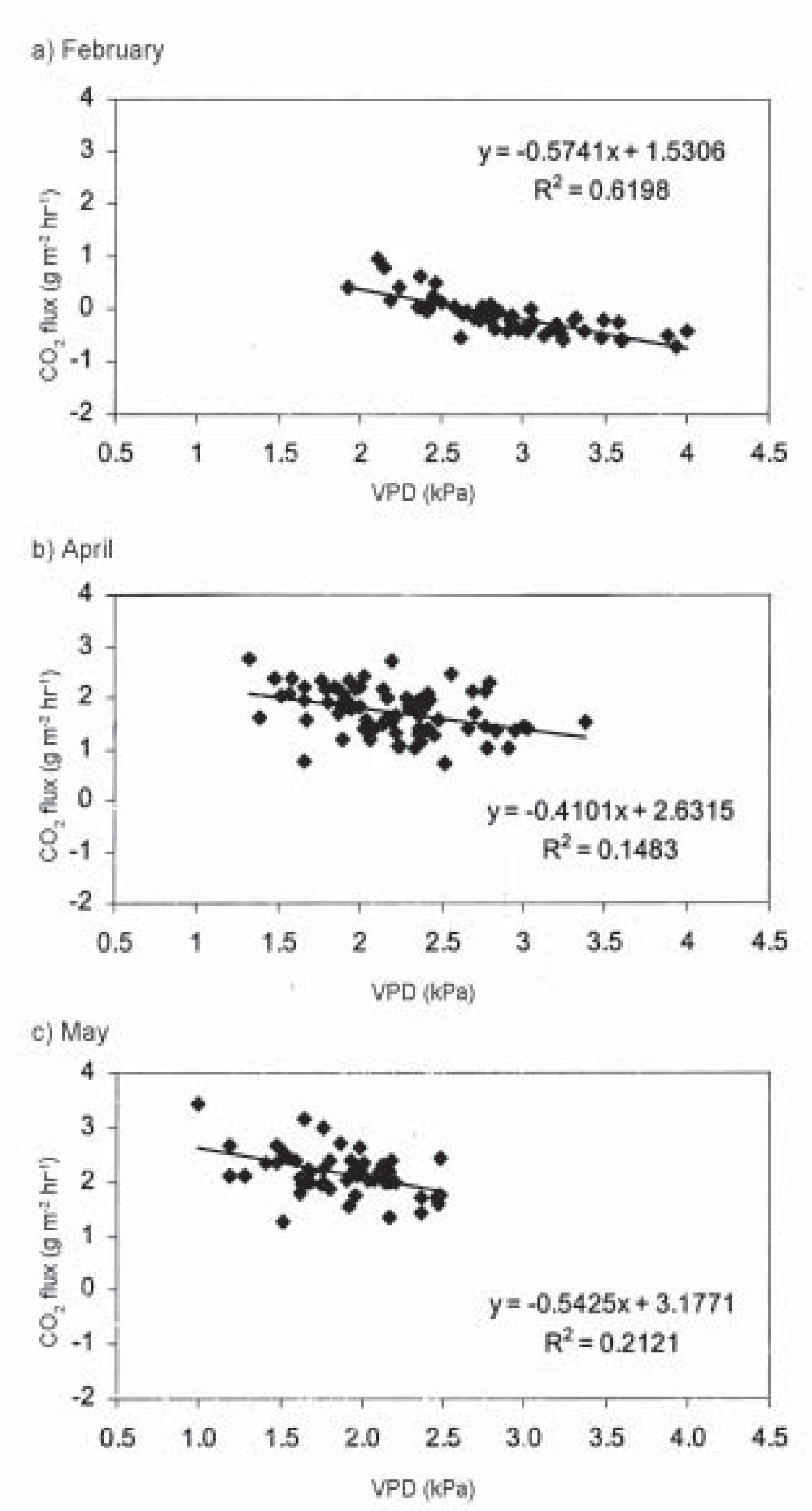

Figure 8. Relationships between hourly CO_2 flux above the canopy and VPD for incident solar radiation levels >700 W m^{-2} in dry (February) and wet (April, May) months. To facilitate comparisons, all graphs are plotted on the same vertical and horizontal scales.

TABLE 7. CORRELATIONS BETWEEN CANOPY CO_2 ASSIMILATION ($g\ m^{-2}\ hr^{-1}$) AND VAPOUR PRESSURE DEFICIT (VPD) (kPa) AND BETWEEN CANOPY CONDUCTANCE AND VPD FOR LEVELS OF SOLAR RADIATION > 700 W m^{-2}*

Month	n	CO_2 assimilation				Canopy conductance			
		α	*b*	r^2	*P*	α	*b*	r^2	*P*
February	53	1.53	-0.57	0.620	0.001	3.68	-0.92	0.383	0.001
April	77	2.63	-0.41	0.147	0.001	13.50	-2.79	0.153	0.001
May	56	3.18	-0.54	0.212	0.001	14.03	-2.29	0.147	0.01
June	35	2.94	-0.45	0.146	0.05	15.00	-3.02	0.224	0.01

Note: *For CO_2 assimilation and canopy conductance, α represents the intercept (assimilation rate or g_c at zero VPD) and *b*, the slope (change in assimilation rate or g_c with VPD) of the linear regressions; n is the number of paired samples.

Canopy conductance responded to VPD in a similar manner to CO_2 uptake, though due to the low conductance values, the slope of the response was least in February (*Table 7*).

The same correlations were performed to examine the effect of VPD on AET and the AET/PET ratio. Results are shown in *Table 8*. The responses of both these related variables to VPD were negative during the dry period in February, non-significant in April and significantly positive during May, and, in the case of AET, during June. This provides a good indication of the changes in availability of water over time. Thus, in wet months, AET increased with VPD, both in absolute terms and as a proportion of the potential rate, perhaps indicating a reduction in the importance of physiological control mechanisms and an increase in direct evaporation of free water from soil and plant surfaces.

Multiple linear regression showed that for the wet months of April, May and June, radiation was the most significant factor affecting CO_2 flux with a substantial increase in r^2 resulting from the combination of radiation and VPD. These two factors accounted for between 20% and 31% of the flux variation. In February, however, the ambient CO_2 concentration (Ca) was the most influential external variable, giving an r^2 of 0.38.

Carbon balance. Attempts to construct a carbon budget for the stand based on CO_2 flux data were impeded by the unreliability of the night-time fluxes. Unlike daytime fluxes, which generally correlated with changes in radiation and vapour pressure deficit, night-time fluxes often showed large hour-to-hour variability. The night-time fluxes were of sufficient magnitude to produce negative carbon balance in all the months. Problems of accurately assessing night-time fluxes have been encountered in previous studies (Price and Black, 1990; Henson, 1995).

Because of this, a modelling approach was adopted based on previous estimates of the total respiratory component of oil palm stands, as summarized by Henson (1995) and Henson and Chang (2000). The main assumptions of the model (see *Appendix* for details) are as follows:

- gross CO_2 assimilation is the sum of daytime CO_2 flux plus daytime respiration;
- total stand respiration is 72% of the gross assimilation of CO_2 [data reviewed by Henson and Chang (2000) gives an average value of 71.2% for eight data sets]; and

TABLE 8. CORRELATIONS BETWEEN ACTUAL EVAPOTRANSPIRATION RATE (AET; mm hr^{-1}) AND VAPOUR PRESSURE DEFICIT (VPD) (kPa) AND BETWEEN THE RATIO OF ACTUAL TO POTENTIAL EVAPOTRANSPIRATION AND VPD FOR LEVELS OF SOLAR RADIATION > 700 W m^{-2}*

Month	n	AET				AET/PET			
		α	*b*	r^2	*P*	α	*b*	r^2	*P*
February	53	0.324	-0.065	0.288	0.001	0.520	-0.110	0.366	0.001
April	78	0.458	0.032	0.010	ns	0.617	0.030	0.004	ns
May	56	0.312	0.131	0.234	0.001	0.559	0.122	0.156	0.01
June	35	0.375	0.082	0.132	0.05	0.600	0.068	0.053	ns

Note: * α represents the intercept (AET or AET/PET at zero VPD) and *b*, the slope (change in AET or AET/PET with VPD) of the linear regressions; n is the number of paired samples.

- respiration increases with temperature with a Q_{10} of 2. Hence, day-time respiration is higher than that of the night.

From mean day and night-time air temperatures (tissues temperatures were not known except in the case of leaflets), the respiration rate in the day was found to average 1.4 times that of the night (the difference between mean day and mean night temperatures was 4.8ºC). Using this ratio, it was possible to roughly apportion the total respiration between day and night and to derive the night-time flux of CO_2 (taken to equal the night-time respiration) from the (measured) daytime flux. Part of the respiration will derive from decomposition of soil organic matter and surface litter. The model assumes a steady state with respect to these components which is a reasonable approximation considering the short time periods involved.

The measured daytime flux and the outputs from the model are shown in *Table 9.* The net assimilation by the canopy during the *wet* months of April to June averaged 5.39 g dry matter m^{-2} day^{-1} (7.9 g CO_2 m^{-2} day^{-1}), or 4.5 times the rate in February. Assuming similar rates to February throughout the January to March dry season, the weighted mean dry matter production (DMP) from January to June was calculated as 3.29 g m^{-2} day^{-1}. Use of alternative values of respiration as a % of gross assimilation ranging from 60% to 75% and day/night respiration ratios between 1.1 and 1.43, caused the estimate of DMP to vary from 2.84 to 4.20 g m^{-2} day^{-1}.

Calculations of the actual DMP of the stand over the first six months of 2004 (*Table 10*) gave a total value of 3.59 g m^{-2} day^{-1}, about 9% higher than the modelled value.

From the modelled oil palm DMP and measured AET, the water use efficiency (mg dry matter g^{-1} H_2O)

TABLE 9. MODELLED CARBON BALANCE OF THE STAND BASED ON MEASURED DAILY DAYTIME DOWNWARD CO_2 FLUX (uptake)

Measuring period	CO_2 downward flux	Net assimilation	Night-time respiration	Daytime respiration	Total respiration	Gross assimilation
	g CO_2 m^{-2} day^{-1}					
14-29 February	3.64	1.76	1.88	2.64	4.52	6.28
3-18 April	12.53	6.05	6.48	9.07	15.35	21.60
9-24 May	19.45	9.39	10.06	14.08	24.15	33.53
9-24 June	17.16	8.28	8.88	12.43	21.30	29.59

TABLE 10. MEAN DRY MATTER PRODUCTION (DMP) BY THE STAND FROM JANUARY TO JUNE 2004 (3.5 to 4 years after planting)*

Component of total DMP	Derivation	DMP		Notes
		g m^{-2} day^{-1}	t ha^{-1} yr^{-1}	
Oil palm shoot	Measured	1.693	6.18	Trunk + fronds
Oil palm root	Measured	0.915	3.34	Includes turnover
Fruit bunches	Measured	0.707	2.58	0.53 * FFB
Ground cover	Estimated	0.274	1.00	Growth restricted by dry season
Total		3.589	13.10	

Note: *The yearly estimates of DMP assume similar conditions and growth rates in the second half to that of the first half of the year and are provided only for comparative purposes. Root DMP includes turnover.

can be estimated. This is shown in *Table 11*. The values are lower than those reported previously, which for a closed canopy, ranged from 1.91 to 2.02 mg DM g^{-1} H_2O (Henson, 1995). The value of WUE would be increased if the DMP of the ground vegetation was included. This was estimated to be about 10% of the palm DMP, almost all likely to have been accumulated during the *wet* months, which would have increased the mean WUE in those months to between 1.28 (April) and 2.0 (May) mg DM g^{-1} H_2O.

TABLE 11. WATER USE EFFICIENCY (WUE) CALCULATED FROM MODELLED OIL PALM DRY MATTER PRODUCTION (DMP) AND MEASURED EVAPOTRANSPIRATION (AET)

Measuring period	DMP g m^{-2} day^{-1}	AET g m^{-2} day^{-1}	WUE mg DM g^{-1} H_2O
14-29 February	1.20	1 269	0.944
3-18 April	4.12	3 544	1.164
9-24 May	6.40	3 523	1.817
9-24 June	5.65	3 155	1.790

GENERAL DISCUSSION

The need to source additional land for oil palm cultivation has led to further interest in the possibility of cultivating areas previously considered unsuitable due to seasonal lack of rainfall. This has highlighted the relative dearth of understanding of the responses and mechanisms underlying yield reductions resulting from inadequate water supply. The present study is part of a programme designed to remedy this deficiency. The site used was chosen due to the regular occurrence of a dry season lasting about three months each year. While it is still too early to assess the impacts of the annual drought on yield (yield being the outcome of developmental processes taking place over a period of up to about three years), previous studies (Henson *et al*., 2005) have categorized changes in soil water content and demonstrated responses by the oil palm in terms of elevated canopy temperatures, reduced rates of water use and reduced spear leaf extension rate.

One of the most immediate responses of plants to water deficit is stomatal closure with a consequent reduction in transpiration and photosynthesis by the canopy. This has been documented previously for oil palm in Malaysia (*e.g*. Corley, 1973; Henson, 1991a; Henson and Chang, 2000) as well as in other countries (Rees, 1961; Potulski, 1990; Dufrene *et al*., 1992; Villalobos *et al*., 1993; Palat *et al*., 2000). The rise in canopy temperature (Henson, 1991b; Henson *et al*., 2005) is a direct consequence of the reduced transpiration rates resulting from stomatal closure.

The specific purpose of the investigation was to assess the impact of the dry season on the gas exchange (transpiration and photosynthesis) of the whole canopy. (Previous measurements made at the site of oil palm leaflet photosynthesis were insufficiently frequent to allow a quantitative assessment of this.) EC, using commercially available open-path sensors, was chosen as the most appropriate technique for this purpose.

The results indicated a marked contrast in gas exchange and surface energy balance between the dry conditions prevailing in February (middle of the dry season) and the wetter conditions found in the following months of April, May and June. In summary, daytime carbon flux to the ground (representing uptake by sinks) was considerably higher in the wet, as compared with the dry period. After correcting the carbon fluxes for the simultaneous transport of heat and water vapour, the CO_2 flux in February during the day was often near to zero or even negative in terms of carbon gain (*Figures 5a* and *6a*). This may appear extreme but has also been observed even in temperate regions, *e.g*. pine plantations (Price and Black, 1990; Jarvis, 1994). The downward flux of CO_2 increased considerably during the wet season and this would have been partly aided by the re-growth of ground vegetation which had died back in the drought.

The very low values of respiration calculated for the dry month of February need confirming. Death of the ground vegetation and the long period of drought preceding measurements probably reduced microbial activity and hence, carbon release, arising from decomposition processes. Plant respiration is known to adjust to some extent to the photosynthetic rate and the reduction in growth would be reflected in lower growth respiration.

There were also dramatic seasonal changes in energy balance (*Figure 4*), associated with the availability of water for evapotranspiration (AET). The sensible heat flux was dominant during the dry, and the latent heat flux (representing the energy used for AET) became the largest component during the wetter months and more typified the conditions expected for the vegetation of humid, tropical regions (Tani *et al*., 2003a, b). A high latent heat flux was also found in a coastal oil palm plantation with abundant water supply (Henson, 1995). The low rate of AET during the dry season, indicated using EC, confirms findings at the same site for the preceding year (Henson *et al*., 2005) based on the soil water balance. However, whereas in February 2004, EC indicated a mean AET/PET ratio of c. 0.3 (*Table 5*), in 2003 the AET/PET calculated from the soil water balance decreased to an even lower level of 0.15 (Henson *et al*., 2005). The available soil water content declined by a similar amount in both years.

The reductions in carbon uptake and evapotranspiration reflect various processes and components of the system. The oil palm canopy covered only about 60% of the ground area at the time of the measurements and micrometeorological methods do not normally permit the separation of the palm from non-palm fluxes. Nevertheless, it can be argued that the palms constituted the dominant sinks and sources in the system since they comprised the bulk of the dry matter and presented the largest evaporative surface. As the oil palms grow, future measurements will become increasingly representative of them, as opposed to the other components of the ecosystem.

The capacity of the EC methodology to yield information that can be used to construct a complete carbon budget is still in doubt. The main problem lies in the uncertainty over the night-time fluxes. Other studies (*e.g.* Price and Black, 1990) have experienced a similar difficulty. Here, we adopted a modelling approach with assumptions based on the best available data. The correspondence between modelled and *measured* dry matter production was good (though note that one item in the *measured* production was also estimated). This exercise needs to be refined in future and improved using data obtained for ground-cover growth and soil respiration.

CONCLUSIONS

These early results provide an indication of the wealth of information that can be obtained using the EC technique but they also point to the need for further data collection to cover transitional periods, especially that from wet to dry seasons when the soil water deficit builds up. Measurements are also needed of the other components of the system including ground cover growth, litter accumulation and soil respiration, so as to construct more accurate carbon budgets.

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APPENDIX

Basic Equations

Fluxes

The eddy correlation or covariance method measures turbulent fluxes directly by correlating fluctuations of vertical wind speed (w) with fluctuations in the transported scalar. The fluxes of sensible heat (H), latent heat (λE), water vapour (E) and CO_2 (Fc) are derived as follows:

$$H = p Cp(\overline{w' T'}) \quad (W\ m^{-2}) \quad (1)$$

$$\lambda E = \lambda(1+\mu\sigma)\,[\overline{w' p_v'} + (\overline{p_v}/\overline{T})\overline{w'T'}] \quad (W\ m^{-2}) \quad (2)$$

$$E = (1+\mu\sigma)\,[\overline{w' p_v'} + (\overline{p_v}/\overline{T})\overline{w'T'}] \quad (g\ m^{-2}\ s^{-1}) \quad (3)$$

$$Fc = \overline{w' p_c'} + (\overline{p_c}/\overline{p_a})\,[\mu/(1+\mu\sigma)]\,E + [(\overline{p_c}/\overline{p})/(Cp\overline{T})]H \quad (mg\ m^{-2}\ s^{-1}) \quad (4)$$

where

p is the density of air containing water vapour ($kg\ m^{-3}$),

Cp, the specific heat capacity of moist air ($J\ kg^{-1}\ K^{-1}$),

W, the vertical wind speed ($m\ s^{-1}$),

T, the absolute temperature (K) = T_a + 273.15, where T_a is the air temperature at measurement height,

λ, the latent heat of vapourization ($J\ kg^{-1}$),

E, the flux of water vapour ($g\ m^{-2}\ s^{-1}$),

μ, the ratio of the molecular masses of dry air and water vapour,

σ, the ratio of the mean densities of water vapour and dry air,

p_v, the density of water vapour ($kg\ m^{-3}$),

p_c, the density of CO_2 ($kg\ m^{-3}$), and

p_a, the density of dry air ($kg\ m^{-3}$),

and the overbars represent a time average and the primes, the instantaneous departures from the means.

Equations 2 to 4 incorporate the corrections derived by Webb *et al.* (1980) for the density effects on water vapour and CO_2 flux arising from the simultaneous transfer of sensible heat and water vapour, as given by Leuning *et al.* (1982).

Energy budget

In the absence of horizontal advection and neglecting minor terms associated with the energy used for photosynthesis or stored by the canopy, the energy budget at the surface can be described as:

$$Rn = H + \lambda E + G \quad (W\ m^{-2}) \quad (5)$$

where Rn is the net radiation and G the ground heat flux.

From this,

$$Rn - G = H + \lambda E \quad (6)$$

where Rn - G represents AE, the available energy ($W\ m^{-2}$).

As the fluxes and Rn and G are measured independently, a comparison of AE so derived with the sum of H and λE provides a check on the measurements.

Aerodynamic and canopy conductance

The canopy aerodynamic conductance (r_{aV}) is largely determined by the wind speed and is the sum of two components, the aerodynamic resistance for momentum (r_{aM}) and the excess resistance due to 'drag' (r_b), where

$$r_{aM} = u/u_*^2 \quad (s\ m^{-1}) \quad (7)$$

$$r_b = \ln(z_o/z_H)/(ku_*) \quad (s\ m^{-1}) \quad (8)$$

and

u is the wind speed at measurement height ($m\ s^{-1}$),

u*, the friction velocity ($m\ s^{-1}$) (given by the eddy flux programme), and

z_o and z_H are the roughness lengths for momentum and heat, respectively. [Here, $\ln(z_o/z_H)$ was taken to equal 1.0 following Jarvis (1994) but a common assumption is that $z_H = 0.2z_o$, giving a value for $\ln(z_o/z_H)$ of 1.61. However, the resultant value of the canopy conductance (see below) was little affected by this ratio.]

In the case of a closed canopy, the canopy or surface conductance to water vapour transfer (g_c) represents the sum total of the stomatal conductances of the various foliage layers within it. In the absence of stomatal measurements, g_c can be derived by rearrangement of the Penman-Monteith combination equation. Various formulations have been given by different authors, *e.g.* Price and Black (1990), Rochette *et al.* (1991), Dolman *et al.* (1991) and Tani *et al.* (2003a).

Here, we mainly followed the treatment of Black and Price (1990) where

$$r_c = [(s\beta/\gamma)-1) * r_{aV}] + [(p_a Cp(e^*(T_a) - e_a)/(\gamma\lambda)] \quad (\mathrm{m\ s^{-1}}) \quad (9)$$

and

r_c is the canopy resistance,
s, the slope of the saturated water vapour pressure with air temperature ($\delta e^*/\delta T_a$),
β, the Bowen ratio ($H/\lambda E$),
γ, the psychometric 'constant' (Pa K^{-1}), and
e_a, the actual water vapour pressure (Pa),

with the other parameters as previously defined.

Finally,

$$g_c = (1/r_c) * 1000 \quad (\mathrm{mm\ s^{-1}}) \quad (10)$$

Modelling Rainfall Interception

The interception of rainfall by the oil palm canopy was derived using a simple model in which the maximum canopy water storage capacity was taken to be 0.135 kg m^{-2} leaf area (0.135 mm). This is an approximate mean based on measurements made by Squire (1984) in Malaysia and Dufrene *et al.* (1992) in the Ivory Coast. It compares with a value of c. 0.123 mm for tropical rain forest [Lloyd *et al.* (1988) as reported by Tani *et al.* (2003b)].

The intercepted rain (P_i) was calculated daily. If the total rainfall (P) exceeded the storage capacity (0.135 * LAI) then P_i = 0.135 * LAI. Otherwise, P_i = P.

Modelling Carbon Balance

When modelling the carbon budget, the following were assumed:

a) that total respiration (R) constitutes a large fraction of the gross carbon assimilation (GA) of 60% to 79% based on published budgets (Henson and Chang, 2000). A mean value of 72% was used here.
b) that the ratio of night/day respiration rate (R_n/R_d) depends on the mean night and day-time air temperatures and the respiratory quotient (Q_{10}). The latter was taken to be 2.0, a value found to apply to maintenance respiration which constitutes the largest fraction of total R. (Growth respiration rate is considered dependent only on biomass increment and composition but the former is in any case likely to be a function of temperature.)
c) that gross CO_2 assimilation (GA) is the sum of daytime CO_2 flux (Fc_d) plus daytime respiration (R_d).
d) that the *true* night-time carbon flux is approximately equal to the night-time respiration.

In the calculations, the components are first expressed as *fractions* of GA. From R = 0.72 * GA and R_n/R_d) = 1.4 (see Results and Discussion), R_n is found to be equal to 0.30 * GA. Thus, R_d = 0.42 * GA. From premise c) above, Fc_d (as a fraction of GA) is equal to 1 – 0.42 = 0.58. From premise d), the night-time flux (Fc_n) = R_n and can be calculated as the product of the *ratio* Fc_n/Fc_d (both expressed as *fractions* of GA) and the actual (measured) Fc_d (= 0.30/0.58 * 12.53 in *Table A1* below). Net assimilation (NA = GA - R) is then equal to Fc_d - Fc_n and GA equals NA + R_n + R_d.

TABLE A1. EXAMPLE OF CALCULATING COMPONENTS OF THE DAILY CARBON BUDGET

Component	Fraction of GA	Value (g CO_2 m^{-2} day^{-1})	Derivation
GA	1.00	21.60	NA + R_n + R_d
NA	0.28	6.05	Fc_d – Fc_n
R_n	0.30	6.48	(Fc_d/Fc_n)*Fc_d
R_d	0.42	9.07	(R_d/R_n)*R_d
R	0.72	15.55	R_d + R_n
Fc_d	0.58	12.53	measured
Fc_n	0.30	6.48	= R_n