The impact of light quality and leaf wetness on photosynthesis in north-west Andean tropical montane cloud forest

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Abstract: Photosynthesis was limited by low-intensity photosynthetically active radiation (PAR) and leaf wetness in a lower montane cloud forest (LMCF) of Cauca, Colombia. Mean PAR intensity remained below the saturation level for leaf-scale net photosynthesis (P_n) throughout the solar day during the wet season and for most of the solar day during the dry season. PAR represented a smaller fraction of total solar radiation ($K\downarrow$) in LMCF than in lowland rain forest (LRF). In LMCF trees and shrubs, mean PAR-saturated P_n ranged from 4.3–10.6 µmol C m^{-2} s^{-1} at 1450 m, and from 3.5–10.2 µmol C m^{-2} s^{-1} at 2150 m. P_n was reduced by abaxial wetness in leaves of some trees and shrubs, and eliminated in others. This study indicates that persistent cloudiness and interception of cloud water by leaves limit LMCF productivity.

Key Words: *Alloplectus*, *Anthurium*, *Cecropia*, *Clusia*, Colombia, Ecuador, light limitation, *Miconia*, PAR, *Psychotria*

INTRODUCTION

A number of factors have been shown to limit the productivity of tropical montane cloud forest (TMCF). These include nutrient limitation (Tanner *et al.* 1990, 1998; Vitousek 1984, Vitousek & Sanford 1986), the chemical effects of soil acidity (Hafkenscheid 2000), low temperature (Kitayama & Aiba 2002), high humidity (Odum *et al.* 1970) and frequent cloud cover (Grubb 1977). There is a great deal of intersite variability in the relative importance of each variable, but the emerging consensus is that productivity is determined through synergistic interaction of multiple controls (Waide *et al.* 1998).

Persistent, frequent or seasonal cloud at the vegetation level is common to all TMCF environments (Bruijnzeel & Proctor 1995). We examined the impact of cloud on the photosynthetic environment of a wet, north-west Andean TMCF in Cauca, Colombia. To determine whether TMCF photosynthetic rate was reduced by light limitation, we compared the intensity of photosynthetically active radiation (PAR) required for maximum net photo-

synthesis (P_n), with mean PAR intensities in TMCF and lowland rain forest (LRF). Secondly, we examined the impact of leaf wetness on P_n in cloud forest vegetation.

STUDY SITES

Three microclimate stations were set up at two field sites, two in a Colombian TMCF and the other in an Ecuadorian LRF. The primary field site was Centro de Estudios Ambientales Tambito (CEAT), a 22.6-km^2 cloud forest reserve in El Tambo, Cauca, Colombia (2°30′N, 77°0′W; 1374–2894 m asl). Mean annual temperature ranged from 11 to 18 °C at CEAT, while precipitation varied from 3600 mm y^{-1} at 1450 m to 7000 mm y^{-1} at 2150 m, based on a 6-y record. Cloud interception by epiphytes contributed approximately 1300 mm y^{-1}, with an additional 560 mm y^{-1} intercepted by tree foliage (González 2000). Mean annual total precipitation was, thus, 5460–8860 mm. Rainfall was heavy from October to May, but peaked in November. The driest month was August, when mean monthly rainfall varied from 100–220 mm. Weather stations were installed in pasture and primary forest, to measure surface radiation balance, PAR, temperature, humidity and rainfall. In addition, soil moisture was measured at the pasture site (2°30′25.20″N, 77°00′1.74″W, 1475 m) and leaf

wetness was monitored at the primary forest station (2°30′45.36″N, 76°59′41.88W, 1600 m). Data were stored on Datataker© loggers (Data Electronics, Australia).

To compare light quantity and quality in TMCF and LRF, surface radiation balance and PAR were also measured at Auca, Napo, Ecuador (0.4°S, 77.0°W, 300 m), 300 km to the south of CEAT, in an area of extensive lowland rain forest. The Auca site, in the western Amazon of Ecuador, has mean annual rainfall of 2860 mm and mean annual temperature of 26 °C.

METHODS

Radiation measurements

Solar radiation (K↓) and PAR were measured continuously at deforested sites at CEAT and Auca, at a height of 1 m. Values were recorded at 10-min intervals and averaged hourly, using silicon cell pyranometers manufactured by Skye Instruments, Llandrindod Wells, Wales (SKP Series). The same type of equipment was used at each site. CEAT readings were taken continuously from 1 August to 31 August and from 1 November to 30 November 1998. The same variables were monitored at the Auca site, from 4 October to 31 December 2000.

The TMCF measurements were taken within the dry season (August) and wet season (November), whereas the Auca measurements were taken during the latter part of the equatorial LRF rainy season. Despite this shortcoming, the hypothesis to be tested was that PAR levels are lower at CEAT than at Auca, even during the dry season. Any bias would, therefore, be toward higher than average readings at CEAT, which leads to even greater confidence, should the light-limitation hypothesis be accepted. While sunlight is most direct in late March and mid-September at CEAT, mean solar radiation intensity is highest in August. The cloudiest and wettest month is November. Average hourly readings were determined for both months, to place upper and lower seasonal bounds on estimates of K↓ and PAR.

Humidity and leaf wetness

A capacitance-based probe (Skye Instruments, Llandrindod Wells, Wales, UK) was used to measure relative humidity (RH) in both pasture and primary forest. The sensors were shielded within a miniature Stevenson screen, to prevent condensation or heating, and were placed at a height of 1.0 m. The probes function at an accuracy of 2% below 95% RH, and at 4% accuracy above 95% RH. Readings were taken every 10 min and averaged

hourly, from 23 June to 14 August 1999 at the pasture site, with missing data from 26 June to 1 July, on 3 July, and 6–8 August. At the primary forest site, measurements were taken every 10 min from 9 September to 9 August 1999 and averaged hourly.

Resistance-based wetness sensors were installed to measure relative 'leaf' wetness in primary forest, from 9 August to 9 September 1999. These wetness sensors are composed of a 5-cm-long, fine circuit-board that undergoes changes in electrical resistance in response to the presence of water droplets (Campbell Scientific, Shepshed, UK; 237F wetness-sensing grids). Changes in resistance alter the voltage passing through the device at a given current. The voltage differences between dry and entirely wet conditions were calibrated to provide estimates of fractional leaf wetness, assuming linear changes in voltage with area wetted. Wetness was sampled at 10-min intervals and averaged hourly. Adaxial (up-facing) sensors were installed at 2.5, 4, 5, 6, 8, 9 and 10 m. A down-facing sensor was placed at a height of 2.5 m to examine the diurnal pattern of abaxial leaf wetness in the TMCF understorey. At 5 m, the sensor was covered in a cylindrical tube to determine the degree of wetting caused by cloud interception alone. The sensors do not have the same surface texture, pubescence, inclination, size, shape or water shedding mechanisms as real leaves. Proportional sensor wetness is, therefore, only intended to provide a relative measure of leaf wetness.

Chamber-based measurements of net photosynthesis

The CIRAS-1™ Differential CO_2/H_2O Infra-Red Gas Analyser was used for net photosynthesis (P_n) measurements, with its 2.5-cm^2 PLC(B) broadleaf cuvette (PP Systems, Hitchin, Hertfordshire, UK). The sampling strategy was to select seven congeners in LMCF (1400–1600 m) and upper montane cloud forest (UMCF; ~ 2150 m), including four trees and three understorey plants. Six of the 7 pairs were confirmed as congeners, but only 7 of 14 species could be identified.

At both elevations, a single individual of each species was used for gas exchange measurements, except where otherwise specified in Table 1. P_n readings were obtained on apparently healthy, fully developed leaves of plants from the families Guttiferae (*Clusia* spp.), Moraceae (*Cecropia* spp.), Melastomataceae (*Miconia* spp.), Rubiaceae (*Psychotria* spp.), Gesneriaceae (*Alloplectus* spp.), Araceae (*Anthurium* spp.) and Arecaceae. In the lower montane cloud forest, the canopy trees examined were *Clusia* sp. LMCF, *Cecropia garciae* Standl., *Miconia* sp. LMCF and *Psychotria racemosa* (Aubl.) Raeusch. Understorey photosynthesis was measured in *Alloplectus teuscheri* (Raymond) Wiehler, *Anthurium*

sp. LMCF, as well as an unidentified palm species. Corresponding plants of the upper montane cloud forest included *Clusia pentandra* Cuatrec., *Cecropia bullata* C. Berg & P. Franco, *Miconia* sp. UMCF and *Psychotria cuatrecasasii* (Standl. ex Steyerm.) C.M. Taylor in the canopy, and *Alloplectus schultzei* Mansfeld, *Anthurium* sp. UMCF and an unidentified palm species in the understorey.

Each tree had a trunk diameter at breast height of at least 5 cm and height of at least 3 m. A different leaf was chosen at least once for every 10 measurements, to obtain a large sample of leaves for each plant. The CO_2 concentration was set to 375 ppm, the approximate ambient level in 1999–2000. Light saturation intensity was defined as the PAR intensity at which modelled P_n reaches 90% of its maximum rate (PAR_{sat}). The Thornley & Johnson (1990) PAR vs. P_n formulation was used for curve fitting, using the non-linear estimation module in Statistica® 5.5 (StatSoft 2000).

Though photosynthesis measurements were taken under natural cloud forest light conditions (N = 2094 measurements), only PAR-saturated readings are reported here (N = 595). During the measurements, soil saturation ratios ($m^3 H_2O m^{-3}$ pore space) remained relatively stable, near the field capacity of 0.53 at the pasture microclimate station at 1450 m. This was due to frequent rainfall and fog drip onto porous soils. Readings were obtained from June to August 1999 with the exception of *Cecropia garciae* (LMCF), for which measurements were taken in February 1999.

To test the hypothesis that photosynthesis is inhibited when a thin film of water covers the abaxial side of LMCF leaves, P_n readings were taken on leaves with the adaxial surface wetted, and then with both surfaces wetted by a fine spray. Readings were also obtained with both surfaces dry, as a control. A fine mist of rainwater was emitted from an atomizer, to wet the leaves as much as possible for 2 min, before the first measurement was taken. More rainwater was applied before subsequent measurements each time the leaf chamber was moved to a new leaf location. For each specimen except *Cecropia garciae*, all measurements were taken on the same two mature, undamaged LMCF leaves. Leaves of *Cecropia garciae* are so large that all measurements were taken on the same leaf, though some supplementary dry-leaf P_n measurements were taken on different portions of the leaf finger to ensure no residual wetness. Some plants were more water-resistant (e.g. *Anthurium* sp. LMCF) than others (e.g. *Clusia* sp. LMCF and *Psychotria racemosa*), so proportional maximum wetness was roughly estimated by sight immediately upon wetting.

Leaf area index (LAI) measurements were taken with the The Delta-T Sunscan® Ceptometer (Delta-T Devices, UK). Measurements were taken at 10-cm intervals, along two 3-m transects in both primary and secondary forest in August 1999.

RESULTS

TMCF microclimate: solar radiation

The frequent cloud cover of TMCF environments reduces mean hourly K↓ relative to LRF, but there is seasonal variation in the strength of this reduction. During the TMCF dry season, K↓ levels were similar at Auca (LRF) and CEAT (LMCF) in the morning, but were greater at Auca during the afternoon (Figure 1a). Maximum recorded K↓ was higher at CEAT at each hour, except 15h00 and 16h00 (not shown). This was likely due to the reduced path length of light at high altitude, as well as scattering and reflection from adjacent clouds.

During the TMCF wet season, mean and maximum hourly K↓ levels were lower than at Auca, and the differences were significant at the 0.05 level (Figure 1a). At CEAT, mean K↓ intensity was greater during the dry season than during the wet season, from sunrise to 14h00. From 15h00 onward, there was no significant difference in K↓ between seasons at the 0.05 level. Maximum recorded values were higher in the dry season, for all hours of the day. In total, $12.0 MJ m^{-2} d^{-1}$
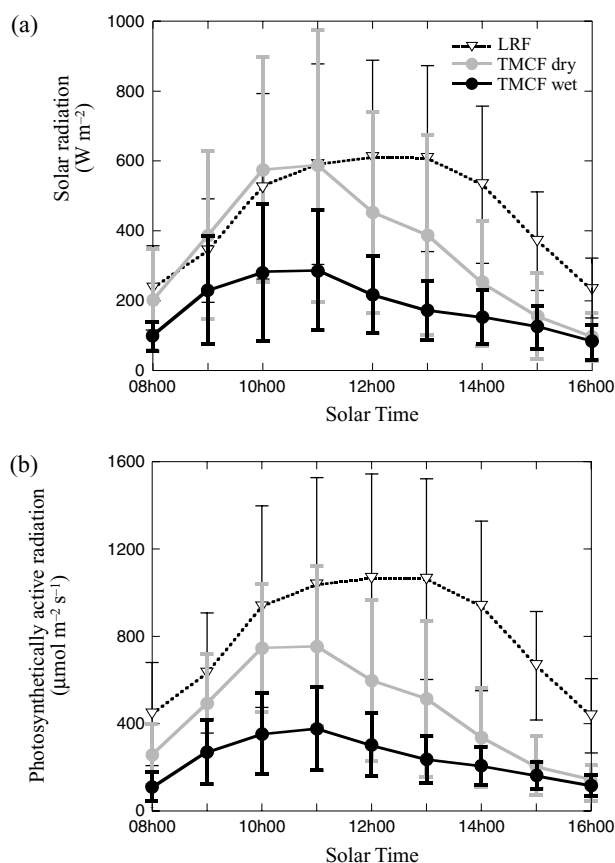

Figure 1. Mean hourly solar radiation intensity (a) and PAR intensity (b) during the TMCF dry season (CEAT), TMCF wet season (CEAT) and in the LRF (Auca).
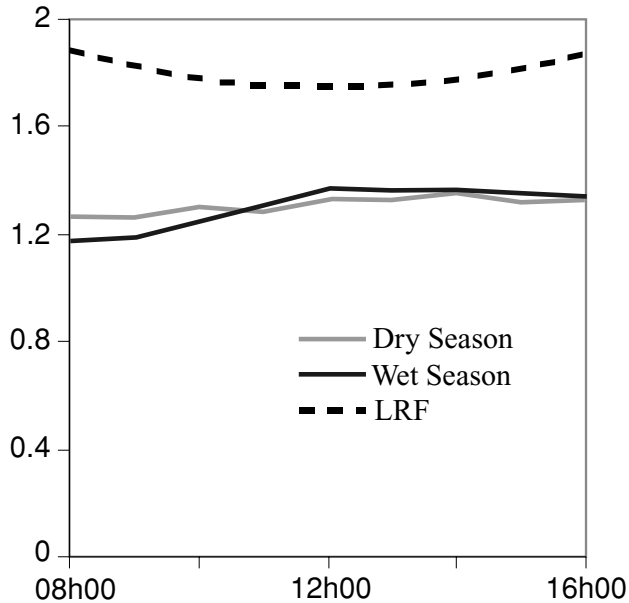
Figure 2. The ratio of PAR (μmol m^{-2}s^{-1}) to K$\downarrow$ (W m^{-2}) at Auca, Ecuador (stippled), and in the TMCF during the dry season (solid grey) and wet season (solid black).

(139.8 W m^{-2}) of K$\downarrow$ was received in the TMCF dry season and 7.6 MJ m^{-2} d^{-1} (73.7 W m^{-2}) was received during the wet season. This compares with mean insolation of 15.6 MJ m^{-2} d^{-1} (181.2 W m^{-2}) at Auca.

Photosynthetically active radiation

PAR: K$\downarrow$ ratios were lower at CEAT than at Auca (Figure 2). Thus, while TMCF K$\downarrow$ levels were lower than in LRF in the afternoon, average PAR was significantly lower at the 0.05 level throughout the day, even during the TMCF dry season (Figure 1b). Maximum recorded PAR levels were also higher at Auca than at CEAT. PAR intensity was significantly higher during the dry season than during the wet season at CEAT except from 15h00 and 16h00 (Figure 1b).

Leaf wetness and humidity

Mean relative humidity (RH) at 1 m remained at or near 100% between 18h00 and 08h00 in the LMCF. On average, RH decreased to a minimum of 78% and 93% at deforested and primary forest sites, respectively. The lowest RH regularly occurred around 11h00. Cloud interception was common during the afternoon and overnight hours, and condensation occurred on clear nights. The nightly wetting pattern, coupled with high humidity, led to significant leaf wetness throughout the solar day within the forest canopy.

Cloud interception caused both adaxial and abaxial wetness, with the latter most evident in the understorey.

Adaxial sensor wetness decreased with height. At night, mean wetness ranged from 58–80% at 2.5–5 m and from 18–69% at 6–9 m. At 10 m, mean wetness was just 14%. Daytime means were 15–20% lower, except at 10 m, where mean values dipped to 8%. Wetness minima occurred between 12h00 and 14h00, and occasionally approached 0%.

Diurnal patterns of 'leaf' wetness, are shown in Figure 3. The thin black line illustrates the pattern of abaxial (down-facing) sensor wetness at 2.5 m. Abaxial leaf wetness is important due to its negative effect on photosynthesis (explained below). The down-facing sensor remained near 65% wetness at night, but mean wetness fell to 40% near midday (Figure 3a), with much lower values occurring on the driest days (Figure 3b). On average, the down-facing sensor was 20% drier than the up-facing sensor at the same level. The solid grey line represents adaxial sensor wetness at 5.0 m, due to cloud interception only (i.e. protected from rainsplash). The solid black line shows the distinct pattern of adaxial sensor wetness near the top of the canopy, where leaves remain relatively dry except during rainfall events.

TMCF photosynthetic processes: net photosynthetic rate

Mean light-saturated photosynthesis (A$_{max}$) for the four canopy species was 9.1 μmol C m^{-2} s^{-1} in the LMCF and 8.2 μmol C m^{-2} s^{-1} in the UMCF. In the understorey, mean A$_{max}$ was 6.8 μmol C m^{-2} s^{-1} in the LMCF and 4.1 μmol C m^{-2} s^{-1} in the UMCF (Table 1). Overall, photosynthesis rates were higher in the LMCF (paired t-test, t = 2.04, P = 0.084). Mean A$_{max}$ ranged from 3.5–10.6 μmol C m^{-2} s^{-1}, suggesting lower photosynthetic capacity than in LRF, where rates range from 5–25 μmol C m^{-2} s^{-1} (Jordan 1985).

Stomatal conductance and transpiration

Leaf stomatal conductance (g$_s$), transpiration rate (E) and water use efficiency (WUE, A$_{max}$/E) are presented for each genus in Table 2. g$_s$ was high in all cases, as was the ratio of internal to ambient CO$_2$ concentration, which varied from 0.74–0.93 at light saturation. g$_s$ was not significantly higher in LMCF than UMCF (paired t-test, t = 1.13, P = 0.303), but E was higher (paired t-test, t = 2.74, P = 0.034). This was the result of higher leaf temperature (T$_l$) and vapour pressure deficit (VPD; Table 3). Due to low evaporative demand, WUE was higher in the UMCF (paired t-test, t = 2.26, P = 0.064).

The effect of leaf wetness on net photosynthesis

A$_{max}$ was not affected by wetting the adaxial surface of LMCF leaves, as would occur during rainfall. However,
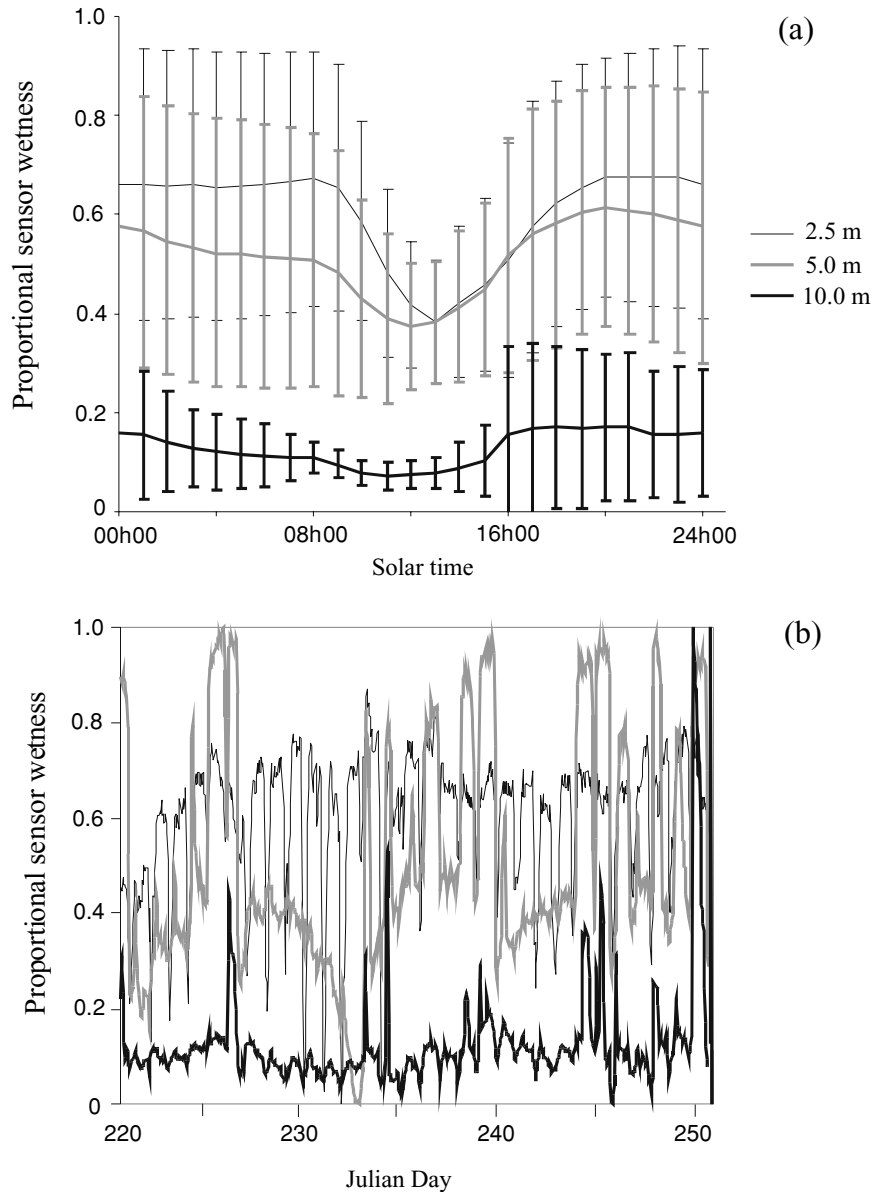
Figure 3. Hourly and diurnal patterns of proportional sensor wetness at CEAT. The sensor at 2.5 m measures abaxial wetness. The sensor at 5.0 m measures adaxial wetness due to cloud interception alone. The sensor at 10 m measures adaxial wetness. Error bars show the standard deviation.

when leaves were wetted both on the adaxial and abaxial sides, as observed during cloud interception events, significant reductions in A_{max} were observed in *Cecropia garciae*, *Anthurium* sp. LMCF and *Miconia* sp. LMCF (Table 4). A near shutdown in measurable P_n was observed in *Psychotria racemosa* and *Clusia* sp. LMCF. Qualitatively, the variation in the photosynthetic response of wetted leaves appears closely tied with the proportion of the leaf that can be wetted with a fine mist. Upon wetting, no dry spots were visible on the abaxial side of *Psychotria racemosa* or *Clusia* sp. LMCF. *Miconia* sp. LMCF and *Cecropia bullata* leaves could be wetted to about 2/3 area, especially near primary and

secondary venation, but *Anthurium* sp. LMCF leaves were quite hydrophobic, so that tiny beads of water covered less than a third of the leaf.

DISCUSSION

TMCF photosynthetic rates are controlled by an array of factors related to microclimate, pedology, physiology, forest stage and functional type. While the relative importance of each control is not fully understood and is known to vary from site to site (Bruijnzeel & Veneklaas 1998), the results of this study indicate that persistent

Table 1. PAR$_{sat}$ and A$_{max}$ in canopy and understorey plants of LMCF and UMCF. N refers to the number of A$_{max}$ measurements, while the number of individuals is in parentheses

Location	Species	Altitude (m)	PAR$_{sat}$ (μmol m^{-2} s^{-1})	A$_{max}$ (mean $\pm$ SD)	N
Canopy	*Cecropia garciae*	1445	950	8.7 $\pm$ 2.2	30 (1)
	Cecropia bullata	2145	950	10.2 $\pm$ 2.2	24 (1)
	Clusia sp. LMCF	1480	600	8.8 $\pm$ 3.4	30 (1)
	Clusia pentandra	2160	670	8.2 $\pm$ 0.5	11 (1)
	Psychotria racemosa	1450	610	10.6 $\pm$ 1.8	15 (1)
	Psychotria cuatrecasasii	2160	910	9.2 $\pm$ 2.2	75 (1)
	Miconia sp. LMCF	1445	560	8.1 $\pm$ 2.0	33 (1)
	Miconia sp. UMCF	2160	420	5.4 $\pm$ 1.2	63 (1)
Understorey	*Anthurium* sp. LMCF	1450	520	9.3 $\pm$ 2.7	178 (15)
	Anthurium sp. UMCF	2160	240	4.5 $\pm$ 1.1	22 (4)
	Alloplectus teuscheri	1600	370	6.6 $\pm$ 0.3	8 (1)
	Alloplectus schulzei	2160	250	3.5 $\pm$ 0.5	51 (1)
	Palm LMCF	1600	220	4.4 $\pm$ 0.5	15 (4)
	Palm UMCF	2160	210	4.2 $\pm$ 1.5	40 (4)

low cloud cover constrains photosynthetic processes by limiting available PAR and wetting the abaxial surface of TMCF foliage.

Radiation quality and quantity

Average K$\downarrow$ was 23% lower at CEAT than in the LRF during the dry season, and 59% lower during the wet season. On an annual basis, mean K$\downarrow$ receipt was comparable with the intensity found at the Arctic Circle in parts of North America and Asia (Budyko 1958). Exacerbating this constraint, is the fact that PAR:K$\downarrow$ ratios were lower in the TMCF, partly because atmospheric transmissivity is lower in the ultraviolet and near-infrared (NIR) wavelengths than for PAR. Selective absorption of PAR and reflectance of NIR by montane vegetation may also have resulted in depletion of the PAR:K$\downarrow$ ratio beneath the cloud deck. As a result, PAR intensity was reduced to just 56% of the LRF level during the dry season and 26% of LRF values during the wet season. Mean PAR does not reach PAR$_{sat}$ levels for canopy trees during the wet season and only reaches PAR$_{sat}$ from 10h00 to 12h00 during the dry season. Previous studies have shown PAR to be reduced by 10–50% in TMCF, relative to LRF (Aylett 1985, Baynton 1968, Bruijnzeel *et al.* 1993, Cavelier & Mejia 1990). Further research is needed to systematically investigate whether poorer light quality is a widespread TMCF characteristic.

PAR is linearly related to productivity at the ecosystem level, for a given carbon yield efficiency of absorbed radiation (Landsberg 1986, Linder 1985, Monteith 1977, Prince & Goward 1995). Much lower productivity would, therefore, be expected in TMCF even if leaf photosynthetic capacity and LAI were similar to LRF. Not only are leaf photosynthetic rates lower on an area basis than in the LRF, but the average LAI at CEAT was 3.6 m^2 m^{-2} at four primary forest sites in the dry season of 1999. This is low compared with LRF, where LAI typically ranges from 4.8–8.5 m^2 m^{-2} (Huttel 1975, Kato *et al.* 1978, Kitayama & Aiba 2002, McWilliam *et al.* 1993, Yamakura *et al.* 1986).

Seasonal light limitation is known to occur even in the LRF, where PAR intensity is much higher. In Parque Nacional Metropolitano, Panama, rainy-season cloud cover reduced photosynthesis in a canopy dominated by *Luehea seemannii* during La Niña (Graham *et al.* 2003), despite the advantage of diffuse radiation for canopy photosynthesis (Gu *et al.* 2002, Roderick *et al.* 2001). The PAR regime of CEAT suggests that the duration of light limitation increases with altitude in wet tropical montane environments and is a persistent feature at LMCF altitudes.

Leaf wetness and photosynthesis in the TMCF

The consistently high g$_s$ measured in each of the paired congeners of this study suggests physiological acclimation to a low VPD environment. However, the benefit of high stomatal conductance is restricted to abaxially dry portions of TMCF leaves. Diffusional limitation of photosynthesis occurs whenever the underside of a leaf is wetted, as a thin film of water reduces gas exchange by covering open stomata (Fogg 1947, Ishibashi & Terashima 1995, Smith & McClean 1989). The diffusion of CO$_2$ in water is one ten-thousandth of its rate in air (Nobel 1991).

Rainfall causes little or no P$_n$ reduction, because only the adaxial surface is wetted and most TMCF leaves are hypostomatous (Roth 1990). Cloud interception and condensation occur mainly on the adaxial surface, but

Table 2. Light-saturated WUE (A_{max}/E; average of individual A and E samples), E (mmol m^{-2} s^{-1}) and g_s (mmol m^{-2} s^{-1}). N refers to the number of measurements, while the number of individuals is in parenthesis

Location	Tree	Factor	Site	Mean	Range	N
Canopy	*Cecropia garciae* and *Cecropia bullata*	WUE	LMCF	2.88 ± 1.08	0.98–5.82	27 (1)
			UMCF	6.13 ± 0.80	5.08–7.19	6 (1)
		E	LMCF	2.99 ± 1.46	0.24–6.33	30 (1)
			UMCF	2.06 ± 0.43	1.35–2.54	6 (1)
		g_s	LMCF	296 ± 99	99–446	20 (1)
			UMCF	438 ± 197	299–577	2 (1)
	Clusia sp. LMCF and *Clusia* cf. *pentandra*	WUE	LMCF	2.43 ± 1.43	0.87–7.50	30 (1)
			UMCF	5.88 ± 2.08	3.07–9.25	11 (1)
		E	LMCF	4.17 ± 1.61	1.16–7.13	30 (1)
			UMCF	1.56 ± 0.54	0.80–2.38	11 (1)
		g_s	LMCF	323 ± 269	64–1121	30 (1)
			UMCF	537 ± 394	107–1168	11 (1)
	Miconia sp. LMCF and *Miconia* sp. UMCF	WUE	LMCF	3.89 ± 1.89	1.18–9.05	33 (1)
			UMCF	3.89 ± 1.77	0.97–8.36	63 (1)
		E	LMCF	2.61 ± 1.44	0.74–6.16	33 (1)
			UMCF	1.65 ± 0.67	0.61–3.50	63 (1)
		g_s	LMCF	300 ± 121	106–622	33 (1)
			UMCF	341 ± 32	233–384	63 (1)
	Psychotria racemosa and *Psychotria cuatrecasasii*	WUE	LMCF	4.63 ± 2.01	2.78–8.03	13 (1)
			UMCF	5.06 ± 2.42	2.01–12.82	75 (1)
		E	LMCF	2.36 ± 1.32	0.24–4.14	15 (1)
			UMCF	2.16 ± 0.92	0.85–4.20	75 (1)
		g_s	LMCF	1327 ± 1187	120–3723	7 (1)
			UMCF	520 ± 438	82–2392	75 (1)
Understorey	*Anthurium* sp. LMCF and *Anthurium* sp. UMCF	WUE	LMCF	3.60 ± 1.37	1.02–9.12	178 (15)
			UMCF	6.63 ± 1.68	3.63–9.75	22 (4)
		E	LMCF	2.73 ± 0.80	0.73–4.98	178 (15)
			UMCF	0.71 ± 0.21	0.40–1.09	22 (4)
		g_s	LMCF	442 ± 208	68–1124	161 (15)
			UMCF	157 ± 100	49–403	22 (4)
	Alloplectus tseucheri and *Alloplectus schulzei*	WUE	LMCF	3.30 ± 1.65	0.99–4.95	8 (1)
			UMCF	3.47 ± 1.03	1.86–6.46	51 (1)
		E	LMCF	1.16 ± 0.35	0.47–1.49	8 (1)
			UMCF	1.09 ± 0.36	0.56–1.96	51 (1)
		g_s	LMCF	421 ± 245	80–684	8 (1)
			UMCF	218 ± 119	70–659	46 (1)
	Palm LMCF and Palm UMCF	WUE	LMCF	5.53 ± 3.35	2.55–13.48	16 (4)
			UMCF	5.34 ± 1.24	2.68–9.09	40 (4)
		E	LMCF	1.07 ± 0.19	0.23–1.49	15 (4)
			UMCF	0.80 ± 0.09	0.39–1.43	41 (4)
		g_s	LMCF	300 ± 141	62–464	15 (4)
			UMCF	175 ± 168	28–669	36 (4)

also on the abaxial side, where the foliar surface is capable of intercepting water droplets at the μm scale (Mason & Andrews 1960). The average reduction in A_{max} resulting from full wetting with a fine mist was 71% in the hypostomatous LMCF leaves of this study.

The fact that P_n inhibition was most severe in leaves lacking water shedding capability is consistent with the laboratory results of Field *et al.* (1998), who demonstrated that the stomatal plugs of *Drimys winteri* var. *chilensis* enabled these leaves to remain dry upon mist application.

Table 3. A comparison of mean, light-saturated WUE, P_n, E, g_s, T_l and VPD in canopy vs. understorey leaves of the LMCF and UMCF, calculated from species averages. WUE_{ind} refers to the average of all individual WUE values, whereas WUE_{tot} is calculated as the quotient of average P_n and average E for each species

Functional type	Site	WUE_{ind} $(P_n/E \times 10^3)$	WUE_{tot} $(P_n/E \times 10^3)$	P_n $\mu mol\ m^{-2}\ s^{-1}$	E $mmol\ m^{-2}\ s^{-1}$	g_s $mmol\ m^{-2}\ s^{-1}$	T_l (°C)	VPD (kPa)
Canopy	LMCF	3.5	3.0	9.1	3.03	562	26.3	0.108
	UMCF	5.2	4.4	8.2	1.86	439	22.9	0.041
Understorey	LMCF	4.1	4.1	6.8	1.65	388	24.6	0.058
	UMCF	5.1	4.7	4.1	0.87	183	20.7	0.049

Table 4. Mean A_{max} in dry leaves and in leaves wetted on both the adaxial and abaxial surfaces (wet leaf)

Species	Average A_{max} ($\mu mol\ m^{-2}\ s^{-1}$)	
	Dry Leaf	Wet Leaf
Anthurium sp. LMCF	7.71 ± 1.27	5.61 ± 0.65
Cecropia garciae	8.11 ± 0.74	4.43 ± 1.08
Miconia sp. LMCF	13.05 ± 1.00	2.09 ± 0.74
Psychotria racemosa	11.57 ± 0.24	0.51 ± 0.31
Clusia sp. LMCF		$P_n \cong 0$ for $0 < PAR$ $< 700\ \mu mol\ m^{-2}\ s^{-1}$

This prevented P_n from being reduced, whereas leaves without plugs remained wet after mist application and displayed P_n reductions of about 40%.

If abaxial surfaces remain wetted for a significant portion of the solar day, net canopy photosynthesis (P_c) could be significantly reduced. Leaf wetness patterns are highly complex, varying by species and decreasing with height within the forest canopy. It is likely that fully exposed, canopy leaves are only slightly affected by leaf wetness, given that average midday wetness is very low even on the adaxial surface. However, mean abaxial sensor wetness remains above 39% at 2.5 m. Letts (2003) suggests that such a pattern of leaf wetness would result in a 6–14% reduction in NPP, using a P_c model that accounts for canopy light extinction and assumes negligible leaf wetness at the crown. Further research is warranted, to assess the effect of abaxial leaf wetness on P_n, the proportion of the abaxial leaf surface wetted and its potential impact on TMCF productivity.

Of all the potential factors controlling photosynthetic rate, the TMCF microclimate is deficient in PAR, the energy source for photosynthesis itself. The montane forests of the Chocó bioclimatic region are exceptionally cloudy and wet, but the findings of this study are consistent with the Massenerhebung effect, as all TMCFs, regardless of elevation, experience frequent ground-level cloud. Persistent cloudiness reduces photosynthetic rates in north-west Andean TMCF through PAR limitation and leaf wetness.

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