

Leaf Gas Exchange in Canopy Species of a Venezuelan Cloud Forest

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ABSTRACT

Tropical cloud forests are considered humid ecosystems with frequent cloud cover down to the ground surface. However, seasonal variation in precipitation may induce short-term water stress. For canopy leaves, this water stress may also be a consequence of large atmospheric vapor pressure deficits. The objective of this work was to study five canopy cloud forest species to determine if there are restrictions to leaf gas exchange as a consequence of seasonality in precipitation and to daily water deficit due to air evaporative demand mainly during maximum incoming radiation hours. Seasonal daily courses of microclimatic variables (air temperature, relative humidity, photosynthetic photon flux density) and plant responses (leaf water potential, stomatal conductance, CO₂ assimilation rates, leaf nitrogen concentration) were measured at 2400 m asl in Monterrey, an intermontane valley of the Venezuelan Andes. A gradient in terms of responses to water stress conditions was observed between the species, with *Clusia multiflora* (a 46% reduction in stomatal conductance between seasons) as the most affected and *Miconia resimoides* (increased stomatal conductance) responding more favorably to slight water stress conditions. If we consider the limitations of water stress and/or light conditions on CO₂ assimilation we may arrange the species into those in which water stress conditions have a greater impact on leaf carbon gain, those where light conditions are determinant and one in which both water stress and light conditions may affect leaf carbon assimilation.

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Key words: *Clusia*; *Guettarda*; leaf carbon assimilation; *Lycianthes*; *Miconia*; *Sapium*; stomatal conductance; tropical montane.

TROPICAL MONTANE CLOUD FOREST is considered a very humid ecosystem with frequent cloud cover down to the ground surface. This cloud influence has two main effects: an increase in water income to the ecosystem via cloud water interception (horizontal precipitation) and a decrease in energy input due to the absorption of sunlight by clouds. Although cloud forests are often considered to experience constant precipitation, they present seasonal variations that may induce a short-term water stress (Bruijnzeel & Veneklaas 1998) and have an effect on physiological processes and growth patterns in plants. And for canopy leaves, this water stress may also occur due to greater atmospheric vapor pressure deficits rather than to changes in soil water conditions. Some plant studies in tropical mountain cloud forests describe constant seasonal soil water availability (Kapos & Tanner 1985, Bruijnzeel *et al.* 1993, Bruijnzeel & Proctor 1995). However, enhanced stomatal resistance in response to increased vapor pressure differences between leaf and air has been reported for a number of tropical cloud forests (Körner *et al.* 1983, Jane & Green 1985, Cavelier 1990). These increases in stomatal resistance were not accompanied by reductions in leaf water potentials (LWPs; Green & Jane 1983). Most literature cited suggests that a high evaporative demand between the forest canopy and the surrounding air is one of the main causes of decrease in stomatal conductance, thereby avoiding large water losses through transpiration. But, at the same time, this may restrict CO₂ assimilation.

The spatial arrangement of the vegetation in cloud forests is characterized by several strata, where the main components are: canopy and subcanopy trees, woody and herbaceous understory plants and a large density and diversity of epiphytes (García-Núñez *et al.* 1995, Ataroff 2001). As a consequence of this forest's complex

structure, steep gradients in different environmental variables, *i.e.*, light, humidity, temperature and CO₂ are observed (Klüge *et al.* 1989, Medina 1995, Engwald 1999). Canopy trees are exposed to a greater air evaporative demand (Mulkey & Wright 1996). As a result, canopy trees in this very humid ecosystem may be subjected to water stress under two different time scales: seasonal variations in precipitation and/or daily water stress produced by a high vapor pressure difference between canopy and air, which may occur under clear skies any time of the year. The objective of this work was to study daily and seasonal stomatal behavior of important species in a tropical cloud forest. We wished to determine if there are restrictions to carbon uptake as a consequence of seasonality in precipitation as well as daily water deficits due to air evaporative demand during periods of maximum incoming radiation.

METHODS

The montane cloud forest occurs between 1700 and 3000 m asl in the Venezuelan Andes (Ataroff 2001). The study area was located at Monterrey, an intermontane valley of the Venezuelan Andean Cordillera (8°37' N, 71°10' W), at 2400 m asl. Annual precipitation is variable, between 1700 and 2700 mm with no climatically dry months, distributed bimodally along the year with lower precipitation from December to February (35–80 mm) and in July (67 mm) and maximum peaks during April and May (290–300 mm) and October (215 mm) (CAECT 1995). Mean monthly temperature is 13.6°C with little variation throughout the year. Low clouds are the main ecological factor acting on these forests most of the year, starting to form early in the afternoon. The vegetation corresponds to an upper montane cloud forest, with a complex structure showing an irregular canopy at 20–25 m and supporting a high diversity of epiphytes (Ataroff 2001). Some frequent tree species found in

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Andean cloud forests and specifically in our study area include: *Clusia multiflora* H. B. & K. (Clusiaceae), *Guettarda steyermarkii* Standl. (Rubiaceae), *Sapium stylare* Muell. Arg. (Euphorbiaceae) and *Miconia resimoides* Cogn. (Melastomataceae) (Ataroff & Rada 2000, Ataroff 2001). These four species and the climber *Lycianthes ferruginea* Bitter (Solanaceae), all with their canopies in the upper strata of the cloud forest, were chosen in this study.

Measurements were done on one individual of each species. These measurements were carried out at 20 m aboveground on a built permanent platform. Daily courses for the wet season (two in May, one in October) and the drier season (one in December, two in January) were carried out simultaneously at *ca* 2-h intervals for each daily course. Air temperature was measured with copper–constantan thermocouples connected to a hand-held digital thermometer (Omega, mod. HH-23, Stamford, CT, U.S.A.) ensuring they were shielded against direct sunlight when the readings were taken. Air humidity was read out from a hand-held digital hygrometer (Omega, mod. RH-200F). And photosynthetic photon flux density (PPFD) was measured with a built-in quantum sensor in the gas exchange system leaf chamber. Plant responses (stomatal conductance [G_s], transpiration [E], CO_2 assimilation rate [A] and LWP) were carried out on different exposed leaves ($N = 6$) for each species. When necessary, during early morning hours, leaves were dried before gas exchange measurements. This was done by carefully blotting both leaf surfaces with absorbent filter paper. G_s , E and A were measured with a portable gas exchange system used in the open mode (LCA-4, ADC Ltd., Hoddesdon, UK), while LWP was measured with a pressure chamber (PMS, Corvallis, OR, U.S.A.). Wet season field measurements of CO_2 assimilation rates at different ambient PPFD were used to construct light response curves. Leaf nitrogen concentration was determined through micro-Kjeldahl analysis for all species during the wet season. A composite sample from five randomly chosen, oven-dried (72 h at 70°C) and ground, adult leaves was obtained for each species. Five replicas were analyzed from each of these samples. Leaf mass per area (LMA) was calculated as the ratio of leaf dry weight (g) per unit area

(cm^2) for 15 randomly selected completely developed leaves. Leaf areas were measured with a Licor (Lincoln, NE, U.S.A.) LI 3100 area meter, dried for 72 h at 70°C and weighed.

RESULTS

Air saturation deficit between seasons was significantly different (Mann–Whitney U test, $P < 0.05$) with a mean of $0.40 \pm .28$ KPa (maximum 0.86 KPa) for the wet and $0.85 \pm .14$ KPa (maximum 1.47 KPa) for the drier seasons. With respect to daily water relations and gas exchange characteristics, important differences in the responses of the studied species were observed (Table 1; Figs. S1–S5). For both seasons, *C. multiflora* showed marked stomatal closure during midday hours (Fig. S1). When one compares the minimum daily stomatal conductance for this species in relation to the mean for the total daily course there was a 59 and 62 percent decrease for wet and drier seasons, respectively (Table 1). Stomatal closure during the wet season occurred even though LWP was relatively high. *Guettarda steyermarkii* showed a pattern of stomatal conductance similar to *C. multiflora* (Fig. S2). Minimum stomatal conductances were observed during midday hours for both wet and drier seasons. However, this decrease in G_s occurred at slightly lower LWP. In addition, this stomatal closure at midday was less severe compared with the previous species (46% and 31% below the mean daily stomatal conductance for wet and drier seasons, respectively). *Sapium stylare* had less pronounced reductions in stomatal conductance during midday hours, especially during the drier season even though LWPs reached more negative values during the afternoon hours (Fig. S3). This species showed the highest stomatal conductances throughout the study. *Lycianthes ferruginea* exhibited stomatal closure toward midday during both seasons as well as the lowest G_s (Fig. S4). For this species, stomatal conductances experienced 52 and 61 percent reductions at midday compared with mean daily stomatal conductances during wet and drier seasons, respectively (Table 1). In contrast to these previous four species, *M. resimoides* showed higher G_s during the drier season, and

TABLE 1. Water relations and gas exchange-related parameters for the wet (WS) and drier (DS) seasons for the five studied species. Mean leaf water potential (Ψ_L , MPa), mean stomatal conductance (G_s , $\text{mmol/m}^2\text{s}$), mean minimum midday stomatal conductance (G_s^{min}), and mean transpiration rate (E , $\text{mmol/m}^2\text{s}$). Means \pm SE. Absolute minimum Ψ_L in parentheses. (Different superscript letters represent significant differences between seasons for each parameter at $P < 0.05$, Mann–Whitney U test.) Means relate to all measurements of different leaves at each 2-h interval for the corresponding sample period.

Species		Ψ_L	G_s	G_s^{min}	E
<i>Clusia multiflora</i>	WS	-0.44 ± 0.06^a (–0.80)	64.2 ± 8.5^a	26.4 ± 1.5^a	0.87 ± 0.12^a
	DS	-0.75 ± 0.08^b (–1.05)	34.6 ± 5.7^b	13.0 ± 1.0^b	0.99 ± 0.25^a
<i>Guettarda steyermarkii</i>	WS	-0.58 ± 0.07^a (–1.30)	70.8 ± 9.2^a	37.9 ± 4.0^a	1.25 ± 0.17^a
	DS	-0.94 ± 0.12^b (–1.40)	49.5 ± 4.0^b	34.2 ± 7.3^a	1.49 ± 0.27^a
<i>Sapium stylare</i>	WS	-0.49 ± 0.08^a (–0.90)	118.4 ± 9.9^a	92.7 ± 5.2^a	1.43 ± 0.14^b
	DS	-0.88 ± 0.10^b (–1.45)	106.2 ± 9.1^a	82.4 ± 1.9^b	2.54 ± 0.33^a
<i>Lycianthes ferruginea</i>	WS	-0.61 ± 0.12^a (–1.20)	45.0 ± 8.2^a	21.6 ± 1.8^a	0.86 ± 0.18^a
	DS	-1.01 ± 0.08^b (–1.45)	33.7 ± 8.5^b	13.0 ± 1.0^b	0.78 ± 0.35^a
<i>Miconia resimoides</i>	WS	-0.65 ± 0.09^a (–1.30)	56.9 ± 9.4^b	65.4 ± 2.9^b	0.99 ± 0.09^b
	DS	-1.01 ± 0.07^b (–1.50)	73.5 ± 8.7^a	81.8 ± 6.3^a	1.58 ± 0.25^a

TABLE 2. Mean photosynthetic capacity-related parameters for the wet (WS) and drier (DS) seasons for the five studied species. Photosynthetic photon flux density (PPFD, $\mu\text{mol}/\text{m}^2\text{s}$), CO_2 assimilation rate (A , $\mu\text{mol}/\text{m}^2\text{s}$), water use efficiency (A/E), substomatal/ambient CO_2 relationship (C_i/C_a). Means \pm SE. (Different superscript letters represent significant differences between seasons for each parameter at $P < 0.05$, Mann–Whitney U test.) Means relate to all measurements of different leaves at each 2-h interval for the corresponding sample period.

Species		PPFD	A	A/E	C_i/C_a
<i>Clusia multiflora</i>	WS	394 \pm 147 ^a	4.52 \pm 0.57 ^a	5.58	0.693 \pm 0.17 ^a
	DS	524 \pm 93 ^a	1.97 \pm 0.53 ^b	1.99	0.637 \pm 0.08 ^b
<i>Guettarda steyermarkii</i>	WS	423 \pm 136 ^b	4.70 \pm 0.58 ^a	3.76	0.779 \pm 0.08 ^a
	DS	871 \pm 75 ^a	4.16 \pm 0.77 ^a	2.79	0.685 \pm 0.06 ^b
<i>Sapium stylare</i>	WS	255 \pm 61 ^b	2.96 \pm 0.55 ^b	2.07	0.798 \pm 0.05 ^a
	DS	614 \pm 102 ^a	4.55 \pm 1.2 ^a	1.79	0.722 \pm 0.06 ^b
<i>Lycianthes ferruginea</i>	WS	316 \pm 121 ^a	2.95 \pm 0.52 ^a	3.43	0.788 \pm 0.05 ^a
	DS	467 \pm 133 ^a	1.84 \pm 0.44 ^b	2.36	0.743 \pm 0.06 ^b
<i>Miconia resimoides</i>	WS	323 \pm 82 ^b	3.02 \pm 0.7 ^b	3.05	0.651 \pm 0.07 ^a
	DS	598 \pm 129 ^a	4.89 \pm 0.88 ^a	3.09	0.656 \pm 0.07 ^a

at the same time it increased toward midday hours (Fig. S5). Seasonally, a gradient in terms of responses to water relations was observed (Table 1). *Clusia multiflora* was the most affected species with respect to G_s , showing a 46 percent decrease from wet to drier seasons. Stomatal control occurred when LWP was relatively high compared with the other four species. However, this species presented similar values for transpiration between seasons due to an increased evaporative demand during the drier season. On the other hand, *M. resimoides* increased G_s toward the drier season, thereby increasing the amount of water lost through transpiration. The other species fell between these two extremes, with *G. steyermarkii* showing a 30 percent decrease, *L. ferruginea* a 25 percent decrease and *S. stylare* an 11 percent decrease in G_s . As a consequence of the seasonal stomatal closure, C_i/C_a ratios were significantly lower during the drier season for all species with the exception of *M. resimoides*. In addition, water use efficiency (A/E) decreased in all species from wet to drier seasons again with the exception of *M. resimoides*.

Mean PPFD was low for all species, mainly during the wet season (Table 2). These low values, together with the effects of stomatal control previously described, gave rise to different effects on mean A between seasons. In the case of *C. multiflora*, even though mean PPFD values were slightly higher during the drier period, A greatly decreased (56%) in this season. CO_2 assimilation of *L. ferruginea* also decreased in the drier season, whereas *G. steyermarkii* maintained similar assimilation values in both seasons. On the other hand, A of *S. stylare* and *M. resimoides* was greater in the drier season.

Maximum A , light compensation point, leaf nitrogen concentration and photosynthetic nitrogen use efficiency for the wet season are presented in Table 3. A significant relationship between nitrogen concentration and maximum assimilation rate was observed when the latter was expressed per unit mass (Fig. 1A),

TABLE 3. Maximum CO_2 assimilation rates per unit leaf area (A_{max}^a , $\mu\text{mol}/\text{m}^2\text{s}$) and weight (A_{max}^m , $\mu\text{mol}/\text{Kg}\text{s}$), light compensation point (Comp Pt, $\mu\text{mol}/\text{m}^2\text{s}$), leaf mass per area (LMA, $\text{g}/\text{m}^2 \pm \text{SE}$), leaf nitrogen concentration (N, $\text{mg}/\text{g DW} \pm \text{SE}$) and photosynthetic nitrogen use efficiency (PNUE, $\mu\text{mol CO}_2/\text{mol N s}$) obtained from wet season data. Values for the first three columns were obtained from PPFD– A curves ($y = a(z+x)/(z+b+x)$); *C. multiflora*: $a = 7.29$, $b = 159$, $z = -25.7$, $R^2 = 0.79$; *G. steyermarkii*: $a = 7.58$, $b = 249$, $z = -13.8$, $R^2 = 0.69$; *S. stylare*: $a = 9.62$, $b = 383$, $z = -21.9$, $R^2 = 0.73$; *L. ferruginea*: $a = 5.29$, $b = 256$, $z = -27.9$, $R^2 = 0.78$; *M. resimoides*: $a = 8.2$, $b = 326$, $z = -20.6$, $R^2 = 0.73$). A_{max}^a and A_{max}^m at PPFD = $1500 \mu\text{mol}/\text{m}^2\text{s}$.

Species	Comp					
	A_{max}^a	A_{max}^m	Pt	LMA	N	PNUE
<i>Clusia multiflora</i>	6.58	21.6	25.7	304.3 \pm 7.2	11.1 \pm 1.6	27.6
<i>Guettarda steyermarkii</i>	6.25	43.7	13.8	148.6 \pm 7.6	18.4 \pm 2.9	32.0
<i>Sapium stylare</i>	7.64	141.0	21.9	54.2 \pm 5.5	31.4 \pm 2.6	62.9
<i>Lycianthes ferruginea</i>	4.51	83.5	27.9	54.0 \pm 6.2	23.6 \pm 1.3	49.6
<i>Miconia resimoides</i>	6.72	96.4	20.6	69.7 \pm 11.2	36.9 \pm 2.0	36.6

while no trend was observed when maximum assimilation per unit area was used. There was also an important correlation between LMA and leaf nitrogen concentration (Fig. 1B). Significant correlations were observed when LMA – A_{max}^m ($R^2 = 0.71$) and G_s (drier season) – A_{max}^m ($R^2 = 0.71$) were compared for all species (relationships not shown, data from Tables 1 and 3).

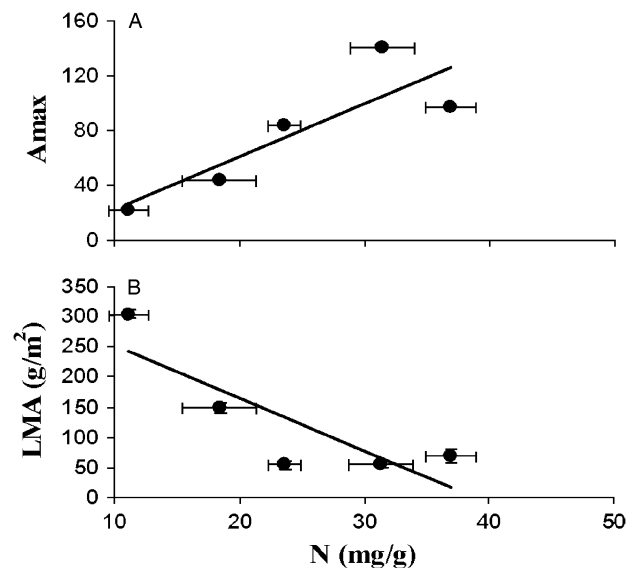


FIGURE 1. Relationship between (A) leaf nitrogen concentration (N_{LEAF} , $\text{mg}/\text{g DW}$) and maximum assimilation rate per unit weight (A_{max}^m , $\mu\text{mol}/\text{Kg s}$) ($A_{\text{max}}^m = 3.874N_{\text{leaf}} - 16.82$, $R^2 = 0.72$) and (B) leaf nitrogen concentration (N_{LEAF} , $\text{mg}/\text{g DW}$) and leaf mass per area (LMA, g/m^2) ($\text{LMA} = -8.7308N_{\text{leaf}} + 338.14$, $R^2 = 0.70$) for all studied species. Bars represent 1 SE from the mean. Data obtained from Table 3.

DISCUSSION

Leaves of canopy species in this particular cloud forest respond in different ways to the water-deficit conditions that may occur both in daily and/or in seasonal terms. A high environmental evaporative demand occurs mainly during the drier season; however, it may also occur during clear days of the wet season. Our results indicate that plants modify the degree of stomatal opening so that large water losses through transpiration are avoided and, therefore, a favorable water status is maintained. Even during the wet season, varied degrees of stomatal control between the species that we studied determine differences in water relations and gas exchange characteristics.

In general, LWPs for all species in our study fell within the values reported for tropical mountain cloud forest tree species in Hawaii (Robichaux & Percy 1980), Jamaica (Kapos & Tanner 1985) and Venezuela (Cavelier 1986). If we compare these and our results with those of lowland rain tropical forests, the latter ones show lower LWPs (Fetcher 1979, Oberbauer & Strain 1985, Rundel & Becker 1987). For stomatal conductances, our results fell in the lower range when compared with those reported for other tropical montane forests (Aylett 1985, Sobrado 2003, Motzer *et al.* 2005). Motzer *et al.* (2005) showed a weak relationship between stomatal conductance and the atmospheric environment for different canopy trees from an Ecuadorian montane forest, concluding that 'diurnal radiation determines the general stomatal status, whereas variable vapor pressure difference accounts for intermediate coordination of stomatal movements throughout the day, thereby limiting the risk of severe water deficits'. A wide range of maximum stomatal conductances have been reported for lowland tropical wet forests (Reich *et al.* 1999, Jührbandt *et al.* 2004, Santiago & Wright 2007). Canopy leaves of most tropical species show a broad array of maximum photosynthetic rates (5–25 $\mu\text{mol}/\text{m}^2/\text{s}$; Mulkey *et al.* 1996). Our results again fall into the lower part of this range.

In agreement with previous findings, our results show a significant correlation between maximum photosynthetic rates (in mass units) and leaf nitrogen concentration. Many other authors have found a strong relationship between leaf nitrogen concentration and maximum CO_2 assimilation: Mulkey *et al.* (1996) for tropical lowland forests, Quilici and Medina (1998) for trees of a disturbed tropical montane forest and Reich *et al.* (1999) for a wide variety of biomes including subalpine, cold temperate, subtropical and tropical rain forests. Reich *et al.* (1999) also found that for all biomes studied leaf N (mass-basis), LMA, G_s and $A_{\text{max}}^{\text{mass}}$ were all positively related, despite differences in climate and evolutionary history, while area-basis A and N were significant with lower P values for the different biomes. More recently, Wright *et al.* (2004), compiling a worldwide data set, correlate different leaf traits among species from a wide variety of vegetation types supporting these previous findings.

There is a large diversity in gas exchange responses to ambient conditions in seasonal terms in a relatively small area of cloud forest. A clear gradient becomes evident in this study, with *C. multiflora* on one end, which may be termed the least tolerant, and *M. resimoides* on the other as the most tolerant. Water stress adaptations have been widely reported for the genus *Clusia* (Nobel 1988, Franco *et al.* 1994, Lüttge 1996). Species with exclusively

crassulacean acid metabolism (CAM) have been found, whereas others are C_3 species. Still other species are facultative, becoming CAM when subjected to water stress and C_3 under favorable conditions (Ting 1985, Sternberg *et al.* 1987). *Clusia multiflora* corresponds to a C_3 species with a reduced capacity to resist water stress, controlling water losses through rigorous stomatal control. In contrast, *M. resimoides* was not affected by ambient water deficit produced during the drier season or during midday hours anytime of the year. On the contrary, stomata open wider, to increase CO_2 concentrations within the leaf to compensate for a more rapid fixation due to higher light conditions, resulting in larger water losses.

Considering daily and/or seasonal responses, for each particular species, in terms of the effect of slight water stress and/or light conditions on gas exchange characteristics, we may arrange the species in this study along a gradient: species in which water stress conditions may have a greater impact on leaf carbon gain (*C. multiflora* and *L. ferruginea*). Both of these species depend on strict stomatal controls that determine lower transpiration rates under the more stressful wet season midday conditions or throughout the whole day under drier season conditions, but at the same time these stomatal restrictions result in a significant reduction in CO_2 assimilation rates. At the other extreme are *S. stylare* and *M. Resimoides*, which maintain or increase stomatal conductances under drier conditions, giving rise to higher transpiration and CO_2 assimilation rates. This indicates that probably light conditions determine lower mean assimilation rates during the wet season. Finally, *G. steyermarkii*, in which both water stress and light conditions seem to slightly affect its gas exchange characteristics. A significant reduction in stomatal opening during the drier season determines a lower transpiration rate, but at the same time, a significantly higher incident radiation helps maintain a high CO_2 assimilation rate compared with the wet season. Apart from the different responses shown by these tropical cloud forest species, low light conditions, mainly during the wet season, may restrict some canopy species from achieving maximum photosynthetic capacity. Cavieres *et al.* (2000) suggest that CO_2 assimilation may be greatly affected by environmental factors such as a low quantum input due to cloud cover most of the year in cloud forest species such as *Podocarpus oleifolius* and *Libanothamus neriifolius* (ex. *Espeletia neriifolius*). Letts and Mulligan (2005) also showed that persistent cloud cover constrains photosynthetic processes by limiting available incoming radiation in Andean montane cloud forests.

Finally, gas exchange characteristics of the studied cloud forest species, as a whole group, did not seem to be affected by stomatal restrictions produced by the mild seasonal water stress. When the results for the different species were pooled and compared between seasons, we found that only mean and minimum LWPs generated significant differences ($P < 0.05$). No significant differences were observed when gas exchange rates (mean and minimum G_s , E and A) between seasons were compared. This result would seem to indicate that milder water stress conditions of cloud forests do not determine environmental reduction of gas exchange characteristics. However, a larger data set may be needed before one can conclude this. Alternatively, our results do suggest that variability in gas exchange characteristics may be found between a few species in a

reduced area of a tropical cloud forest. In conclusion, canopy trees of cloud forests confront daily and seasonal water deficit in different ways, and depending on how each species faces this problem, implications on gas exchange and more particularly on CO₂ assimilation also become important. Therefore, ambient seasonality and interspecific variability are important factors to be considered in leaf carbon gain studies of tropical cloud forests.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Representative daily courses for wet and drier seasons for *Clusia multiflora*.

FIGURE S2. Representative daily courses for wet and drier seasons for *Guettarda steyermarkii*.

FIGURE S3. Representative daily courses for wet and drier seasons for *Sapium stylare*.

FIGURE S4. Representative daily courses for wet and drier seasons for *Lycianthes* sp.

FIGURE S5. Representative daily courses for wet and drier seasons for *Miconia resimoides*.

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