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 reiszmorensis (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.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

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

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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 Mull. 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) to ambient PPFD were used to construct light response curves. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper. This was done by carefully blotting both leaf surfaces with absorbent filter paper. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper. When necessary, during early morning hours, leaves were dried blotting both leaf surfaces with absorbent filter paper.

### RESULTS

Air saturation deficit between seasons was significantly different (Mann–Whitney U test, \( P < 0.05 \)) with a mean of 0.40 ± 28 KPa (maximum 0.86 KPa) for the wet and 0.85 ± 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, Clusia 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 LWP 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

| Species                | \( \Psi_L \) (MPa) | \( G_s \) (mmol/m²s) | \( G_s^{min} \) (mmol/m²s) | \( E \) (mmol/m²s) |
|------------------------|---------------------|----------------------|-----------------------------|-------------------|
| Clusia multiflora      | –0.44 ± 0.06* (–0.80) | 64.2 ± 8.5*          | 26.4 ± 1.5*                 | 0.87 ± 0.12*     |
| Guettarda steyermarkii | –0.75 ± 0.08* (–1.05) | 34.6 ± 5.7b          | 13.0 ± 1.0b                 | 0.99 ± 0.25*     |
| Sapium stylare         | –0.58 ± 0.07* (–1.30) | 70.8 ± 9.2*          | 37.9 ± 4.0*                 | 1.25 ± 0.17*     |
| Lycianthes ferruginea  | –0.94 ± 0.12* (–1.40) | 49.5 ± 4.0b          | 34.2 ± 7.3*                 | 1.49 ± 0.27*     |
| Miconia resimoides     | –0.49 ± 0.08* (–0.90) | 118.4 ± 9.9*         | 92.7 ± 5.2*                 | 1.43 ± 0.14a     |
|                        | –0.88 ± 0.10* (–1.45) | 106.2 ± 9.1*         | 82.4 ± 1.9b                 | 2.54 ± 0.33*     |
|                        | –0.61 ± 0.12* (–1.20) | 45.0 ± 8.2*          | 21.6 ± 1.8*                 | 0.86 ± 0.18*     |
|                        | –1.01 ± 0.08* (–1.45) | 33.7 ± 8.5b          | 13.0 ± 1.0b                 | 0.78 ± 0.35*     |
|                        | –0.65 ± 0.09* (–1.30) | 56.9 ± 9.4a          | 65.4 ± 2.9b                 | 0.99 ± 0.09b     |
|                        | –1.01 ± 0.07* (–1.50) | 73.5 ± 8.7a          | 81.8 ± 6.3a                 | 1.58 ± 0.25*     |

* Absolute minimum \( \Psi_L \) in parentheses. (Different superscript letters represent significant differences between species 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.
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, μmol/m²s), CO₂ assimilation rate (A, μmol/m²s), water use efficiency (A/E), substomatal/ambient CO₂ relationship (C/Cₐ). Mean ± 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 (μmol/m²s) | A (μmol/m²s) | A/E | C/Cₐ |
|------------------|-----------------|--------------|-----|------|
| Clusia multiflora| 394 ± 147a 4.52 ± 0.57a | 5.58 0.693 ± 0.17a |      |
| Sapium stylare   | 524 ± 93b 1.97 ± 0.53b | 1.99 0.637 ± 0.08b |      |
| Guettarda steyermarkii | 423 ± 136b 4.70 ± 0.58b | 3.76 0.779 ± 0.08b |      |
| Lycianthes ferruginea | 871 ± 75b 4.16 ± 0.77b | 2.79 0.685 ± 0.06b |      |
| Miconia resimoides | 255 ± 61b 2.96 ± 0.55b | 2.07 0.798 ± 0.05b |      |
|                  | 614 ± 102a 4.55 ± 1.2a | 1.79 0.722 ± 0.06a |      |
|                  | 316 ± 121a 2.95 ± 0.52a | 3.43 0.788 ± 0.05a |      |
|                  | 467 ± 133a 1.84 ± 0.44a | 2.36 0.743 ± 0.06a |      |
|                  | 323 ± 82b 3.02 ± 0.78b | 3.05 0.651 ± 0.07b |      |

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 Gᵣ 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 Gᵣ 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 Gᵣ. As a consequence of the seasonal stomatal closure, C/Cₐ 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, give 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. CO₂ 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), 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 – Aₘₐₓ (R² = 0.71) and Gᵣ (drier season) – Aₘₐₓ (R² = 0.71) were compared for all species (relationships not shown, data from Tables 1 and 3).

TABLE 3. Maximum CO₂ assimilation rates per unit leaf area (Aₘₐₓ, μmol/m²s) and weight (Aₘₐₓ, μmol/Kg), light compensation point (Comp Pt, μmol/m²s), leaf mass per area (LMA, g/m² ± SE), leaf nitrogen concentration (N, mg/g DW ± SE) and photosynthetic nitrogen use efficiency (PNUE, μmol CO₂/mol N) obtained from wet season data. Values for the first three columns were obtained from PPFD–A curves (y = a(x+b))/x. C. multiflora: a = 7.29, b = 159, z = –25.7, R² = 0.79; G. steyermarkii: a = 7.58, b = 249, z = 13.8, R² = 0.69; S. stylare: a = 9.62, b = 383, z = –21.9, R² = 0.73; L. ferruginea: a = 5.29, b = 256, z = –27.9, R² = 0.78; M. resimoides: a = 8.2, b = 326, z = –20.6, R² = 0.73. Aₘₐₓ and Aₘₐₓ at PPFD = 1500μmol/m²s.

| Species          | Aₘₐₓ (μmol/m²s) | Aₘₐₓ (μmol/Kg) | Comp Pt (μmol/m²s) | LMA (g/m² ± SE) | N (mg/g) | PNUE |
|------------------|----------------|---------------|-------------------|-----------------|---------|------|
| Clusia multiflora| 6.58           | 21.6          | 25.7              | 304.3 ± 7.2     | 11.1 ± 1.6 | 27.6 |
| Guettarda steyermarkii | 6.25           | 43.7          | 13.8              | 148.6 ± 7.6     | 18.4 ± 2.9 | 32.0 |
| Sapium stylare   | 7.64           | 141.0         | 21.9              | 54.2 ± 5.5      | 31.4 ± 2.6 | 62.9 |
| Lycianthes ferruginea | 4.51           | 83.5          | 27.9              | 54.0 ± 6.2      | 23.6 ± 1.3 | 49.6 |
| Miconia resimoides | 6.72           | 96.4          | 20.6              | 69.7 ± 11.2     | 36.9 ± 2.0 | 36.6 |

FIGURE 1. Relationship between (A) leaf nitrogen concentration (Nₐₑᵃᶠ, mg/g DW) and maximum assimilation rate per unit weight (Aₘₐₓ, μmol/Kg) (Aₘₐₓ = 3.874Nₐₑᵃᶠ – 16.82, R² = 0.72) and (B) leaf nitrogen concentration (Nₐₑᵃᶠ, mg/g DW) and leaf mass per area (LMA, g/m²) (LMA = 8.7308Nₑᵃᶠ + 338.14, R² = 0.70) for all studied species. Bars represent 1SE 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 & Pearcy 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, Motzet et al. 2005). Motzet 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, Juhrbandt et al. 2004, Santiago & Wright 2007). Canopy leaves of most tropical species show a broad array of maximum photosynthetic rates (5–25 μmol/m²/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 CO₂ 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, Gₛ and Aₘ₅ₐₓ 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 Clusia florifera 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, Lützge 1996). Species with exclusively crassulacean acid metabolism (CAM) have been found, whereas others are C₃ species. Still other species are facultative, becoming CAM when subjected to water stress and C₃ under favorable conditions (Ting 1985, Sternberg et al. 1987). Clusia florifera corresponds to a C₃ 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 CO₂ 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. florifera 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 CO₂ assimilation rates. At the other extreme are S. stylare and M. Resioides, which maintain or increase stomatal conductances under drier conditions, giving rise to higher transpiration and CO₂ 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 CO₂ 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 CO₂ 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. Epeletia 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 Gₛ, 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 reimoides.

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