

# Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes

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**Summary** We investigated tree water relations in a lower tropical montane rain forest at 1950–1975 m a.s.l. in southern Ecuador. During two field campaigns, sap flow measurements (Granier-type) were carried out on 16 trees (14 species) differing in size and position within the forest stand. Stomatal conductance ( $g_s$ ) and leaf transpiration ( $E_l$ ) were measured on five canopy trees and 10 understory plants. Atmospheric coupling of stomatal transpiration was good (decoupling coefficient  $\Omega = 0.25–0.43$ ), but the response of  $g_s$  and  $E_l$  to the atmospheric environment appeared to be weak as a result of the offsetting effects of vapor pressure deficit (VPD) and photosynthetic photon flux (PPF) on  $g_s$ . In contrast, sap flow ( $F$ ) followed these atmospheric parameters more precisely. Daily  $F$  depended chiefly on PPF sums, whereas on short time scales, VPD impeded transpiration when it exceeded a value of 1–1.2 kPa. This indicates an upper limit to transpiration in the investigated trees, even when soil water supply was not limiting. Mean  $g_s$  was  $165 \text{ mmol m}^{-2} \text{ s}^{-1}$  for the canopy trees and about  $90 \text{ mmol m}^{-2} \text{ s}^{-1}$  for the understory species, but leaf-to-leaf as well as tree-to-tree variation was large. Considering whole-plant water use, variation in the daily course of  $F$  was more pronounced among trees differing in size and crown status than among species. Daily  $F$  increased sharply with stem diameter and tree height, and ranged between 80 and  $120 \text{ kg day}^{-1}$  for dominant canopy trees, but was typically well below  $10 \text{ kg day}^{-1}$  for intermediate and suppressed trees of the forest interior.

**Keywords:** atmospheric coupling of transpiration, stomatal control, tree water relations, tropical mountain.

## Introduction

Tropical montane forests (TMF) are still among the least understood and investigated terrestrial ecosystems in the world. In particular, little is known about their water and nutrient cycles (Bruijnzeel 1990, 2001, Zotz et al. 1998, Bussmann 2001). Most available data on evapotranspiration and TMF

water budgets are based on catchment studies (e.g., Edwards 1979, Cavelier et al. 1997, Schellekens 2000, Wilcke et al. 2001), whereas information on water fluxes and gas exchange of individual trees in montane environments is scarce. Besides the pioneering work of Kline et al. (1970) in a TMF and Weaver (1975) in an elfin forest (both in Puerto Rico), more recently, Bruijnzeel and Proctor (1995), Santiago et al. (2000) and (D. McJannet and P. Redell, CSIRO Land and Water, Australia, unpublished results) have presented sap flow data for montane forest trees on Krakatau (Indonesia), Hawaii and in northern Australia, respectively. The study of Zotz et al. (1998) in Panama yielded physiological information on water status and hydraulic architecture.

The research presented here formed part of a multidisciplinary project conducted in the northern part of Podocarpus National Park in the southern Ecuadorian Andes (Beck and Müller-Hohenstein 2001). Our study was undertaken to obtain information on the stomatal behavior and transpiration of lower TMF trees; specifically, we combined single-leaf porometry and sap flow measurements to evaluate whole-tree water use. Porometry is an excellent field method because it provides reliable results on stomatal characteristics, despite high leaf-to-leaf variability, a limited number of measurements (highly labour intensive) and the difficulties of crown access (Lange et al. 1976, Schulze and Küppers 1979, Turner et al. 1984). In contrast, the measurement of sap flow is a well-proven method for determining whole-tree water fluxes, at least in the medium term (Granier et al. 1996a, Oren et al. 1996, Andrade et al. 1998, Köstner et al. 1998, Wullschlegel et al. 1998).

With increasing altitude, temperature as well as the partial pressures of air, water vapor and  $\text{CO}_2$  decrease, whereas solar radiation flux and the incidence of cloud cover may increase (Whiteman 2000). This leads to the question of whether there are significant differences in ecophysiology and water consumption between TMF trees and those of tropical lowlands. We hypothesized that mean values of stomatal conductance

and tree transpiration are lower in TMF trees than in lowland forest trees, primarily because of frequent cloud cover (low light) and high atmospheric humidity. To test this hypothesis, we investigated the atmospheric influence on stomatal conductance and transpiration, and quantified mean values for different tree species in the forest.

## Materials and methods

### Study site

The study area is located within a native lower montane rain forest of the Reserva Biológica San Francisco in the southern Ecuadorian Andes (3°58' S, 79°04' W; cf. Beck and Müller-Hohenstein 2001). Measurements were made in two forest plots: a pilot plot (200 m<sup>2</sup>) was situated at 1975 m a.s.l. on a northwest-facing slope, whereas the main study plot was located about 300 m southwest of the pilot plot at 1950 m a.s.l. and comprised 480 m<sup>2</sup> of steep terrain (up to 40–45°, NNW-oriented). Both study plots were covered with a tropical lower montane forest (as defined by Richards 1996, Bruijnzeel and Hamilton 2000) or, as characterized by Bussmann (2001), a montane broad-leaved (*Ocotea–Nectandra*) forest. Abundance of phanerogams belonging to families typical for the Amazonian lowlands (e.g., Cyclanthaceae, Lauraceae, Melastomataceae) was high, and frequency of epiphytes and lianas was moderate compared with at higher altitudes (Fingerle 1999). Species composition of the two stands differed slightly, especially with respect to the most prominent tree species within this altitudinal range (Bussmann 2001), with *Alzatea verticillata* Ruiz & Pav. (Alzateaceae) present only at the pilot plot. Mean canopy height was 18 and 14 m at the main and the pilot plot, respectively. Dominant tree species with extensive crowns built up the overstory layer at the main plot at 14–18 m (pilot plot: 11–14 m). Because of the difficulties of defining boundaries below the overstory, a further structural subdivision of the forest into a midcanopy layer (main plot: 6–14 m; pilot plot: 7–11 m) and a subcanopy stratum (main plot: 2.5–6 m, pilot plot: 2–7 m) remained largely subjective. Understory layers consisted of herbs, ferns, seedlings and juvenile trees up to 2–2.5 m. At the main and pilot plots, leaf area index (LAI) was 6.4 and 5.6, and stand basal area was 25.9 and 41.6 m<sup>2</sup> ha<sup>-1</sup> (based on trees with stem diameter (DBH) > 10 cm), respectively (for further details see Ohlemacher 2001 and Motzer 2003).

According to regional climate data reported by Paul Emck (Institute of Geography, University of Erlangen, Germany, unpublished observations), annual precipitation is 2067 mm (period 1998–2002). The rainy season is from April to June (maximum rainfall in May: 257 mm), whereas the drier period is between November and January (minimum rainfall in November: 90 mm). Mean annual (1999–2002) air temperature is 15.5 °C, varying from 14.5 (July) to 16.2 °C (November). On dry days, temperatures can exceed 25 °C. Air humidity is usually high, and nighttime saturation associated with dew deposition on plant surfaces is common. Low cloud or dense fog is infrequent so that horizontal precipitation contributes less

than 5% to annual precipitation at altitudes between 1800 and 2000 m a.s.l. (R. Rollenbeck, University of Marburg, Germany, personal communication).

### Environmental measurements

During the pilot study (November 1999–February 2000), methodological approaches were tested and preliminary ecophysiological data were collected. During the main phase of the investigation, ecophysiological studies (September 2000–March 2001) were supplemented with detailed microclimatological measurements within and above the forest stand (until February 2002).

Forest microclimate was measured along a vertical profile with sensors attached to a steel-wire support system suspended from a branch of *Trichilia guianensis* Klotzsch (Meliaceae), a dominant canopy tree 18 m high. Air temperature and humidity (HMP35, Vaisala, Vaisala, Helsinki, Finland), photosynthetically active radiation (PAR) (SKP215, Skye Instruments, Powys, U.K.) and wind speed (Vector Instruments, Alfreton, U.K.) were measured 4, 8 and 13 m above the forest floor. Additionally, above-canopy microclimate was recorded with a set of sensors on a telescoping crossbar mount, attached to the uppermost robust branch of the same *T. guianensis* tree, and reaching about 2 m above the vegetation surface. The telescopic mounting system supported the following lightweight instruments: a 50Y temperature and humidity probe (Vaisala), an LI-200-SA short-wave radiation sensor (Li-Cor, Lincoln, NE) and an NRLite net radiation sensor (Kipp and Zonen, Delft, The Netherlands). Data were recorded as 5-min means from 30-s sampling intervals with a CR10X data logger (Campbell Scientific, Shephed, U.K.).

### Stomatal conductance

Water vapor loss and stomatal conductance ( $g_s$ ) of individual leaves were obtained by porometry (Li-Cor LI-1600 steady-state porometer). Tree crowns were accessed by the single-rope climbing technique using mechanical ascenders and a seat-harness. Measurements could thus be obtained only within the central crowns of five accessible canopy trees and 10 understory individuals (Table 1). The porometric data set comprised about 2000 measurements, representing 21 days between January and March 2001. Measurements were made on the abaxial leaf surface after it had been determined that the  $g_s$  of the upper leaf surface was negligible.

Calculation of leaf transpiration ( $E_l$ ) from porometer readings can lead to serious overestimations (Meinzer et al. 1995), because the constantly ventilated chamber of the porometer creates an abnormally high boundary layer conductance ( $g_b \approx 2250 \text{ mmol m}^{-2} \text{ s}^{-1}$ ). Therefore, when calculating  $E_l$ ,  $g_b$  was replaced by a value more typical of natural conditions, which was estimated by the expression introduced by McDermitt (1990):

$$g_b = C \left( \frac{u}{d} \right)^{0.5} \quad (1)$$

Table 1. Porometric measurements at the main plot of the investigated canopy and understory trees. Abbreviations: DBH = stem diameter at breast height;  $H$  = tree height;  $g_s$  = mean stomatal conductance;  $E_1$  = leaf transpiration rate; and  $\Omega$  = decoupling coefficient for leaves. Standard deviations are in parentheses.

Species	Family	DBH (cm)	$H$ (m)	$g_s$ (mmol m <sup>-2</sup> s <sup>-1</sup> )	$E_1$ (mmol m <sup>-2</sup> s <sup>-1</sup> )	$\Omega$
<b>(a) Canopy trees</b>						
<i>Ruagea cf. pubescens</i> H. Karst.	Meliaceae	38.2	18.0	95.9 (73.3)	0.84 (0.43)	0.25 (0.2)
<i>Psychotria brachiata</i> Ruiz & Pav.	Rubiaceae	6.1	6.0	83.2 (47.1)	0.52 (0.29)	0.27 (0.18)
<i>Trichilia guianensis</i> Klotzsch	Meliaceae	40.4	18.0	289.3 (232.4)	1.60 (1.08)	0.43 (0.21)
<i>Naucleopsis</i> sp.	Moraceae	11.1	12.0	103.5 (80.9)	0.91 (0.69)	0.27 (0.24)
<i>Hedyosmum anisodorum</i> Todzia	Chloranthaceae	10.8	13.0	233.2 (164.8)	1.44 (0.89)	0.37 (0.21)
<b>(b) Understory trees</b>						
<i>Guarea</i> sp.	Meliaceae	2.3	3.0	44.6 (12.4)	0.66 (0.44)	0.29 (0.18)
Unidentified species		4.3	2.0	116.3 (99.1)	0.41 (0.29)	0.26 (0.31)
<i>Palicourea</i> sp.	Rubiaceae	1.4	2.0	106.8 (80.0)	0.51 (0.31)	0.24 (0.16)
<i>Piper</i> sp.	Piperaceae	0.8	2.0	65.9 (54.4)	0.47 (0.39)	0.13 (0.09)
Unidentified species		0.8	2.6	100.3 (69.6)	0.62 (0.29)	0.23 (0.19)
Unidentified species		1.3	2.5	73.9 (63.7)	0.46 (0.29)	0.19 (0.11)
Unidentified species		1.9	2.5	93.1 (93.0)	0.47 (0.33)	0.25 (0.26)
<i>Palicourea</i> sp.	Rubiaceae	2.2	3.3	106.0 (82.0)	0.62 (0.34)	0.23 (0.12)
Unidentified species		1.9	3.0	120.1 (103.5)	0.48 (0.43)	0.28 (0.17)
Unidentified species	Arecaceae	0.4	1.2	42.9 (30.0)	0.32 (0.23)	0.21 (0.11)

where  $u$  is wind speed (m s<sup>-1</sup>),  $d$  is mean leaf extension (m) and  $C$  is a constant ( $\approx 0.24$  mmol m<sup>-2</sup>; see McDermitt 1990 and Motzer 2003 for further discussion).

Stomatal control of  $E_1$  depends largely on the  $g_b:g_s$  ratio. It is high only when the leaf boundary layer is thin ( $g_b > g_s$ ), coupling the leaf surface to vapor pressure and the evaporative demand of the surrounding air. When  $g_b$  is low compared with  $g_s$ , a local equilibrium of humidity may establish within the boundary layer, leading to partial decoupling of  $E_1$ . The extent of atmospheric coupling is quantified in terms of a dimensionless decoupling coefficient,  $\Omega$ , as introduced by McNaughton and Jarvis (1983):

$$\Omega = \frac{\epsilon_* + 1}{\epsilon_* + 1 + \frac{g_b}{g_s}} \quad (2)$$

where  $\epsilon_*$  is the ratio of the slope of the relationship between saturation vapor pressure and temperature ( $d\epsilon_*/dT$ ) to the psychrometric constant, and  $\Omega$  is between 0 and 1, with 0 representing full stomatal control of  $E_1$ .

### Sap flow

To estimate individual tree water use, xylem sap flow was measured by the thermal dissipation method (Granier 1985). Following the original design of the Granier-sensor, sap flow gauges (UP GmbH, Cottbus, Germany), consisting of two needle-probes (length: 20 mm, diameter: 2 mm), were inserted, one above the other, horizontally into the sapwood of the tree stem. The upper probe is heated continually, creating a temperature difference with respect to the lower unheated probe, which provides the reference temperature of the sapwood. The

temperature difference is inversely correlated with sap flux density (volume per unit sapwood area). Sap flow was measured on 16 trees of different species and crown position within the forest. To account for sap flow variations caused by sapwood heterogeneity, additional sensors were inserted in different azimuthal stem positions and in the adjacent depth interval of 20–40 mm (Table 2).

Calculation of sap flux density,  $J_s$  (g m<sup>-2</sup> s<sup>-1</sup>), followed the equation developed by Granier (1985, 1987):

$$J_s = 119 \left( \left[ \frac{\Delta T_M}{\Delta T} \right] - 1 \right)^{1.231} \quad (3)$$

where  $\Delta T$  is the temperature difference between the heated and unheated probe and  $\Delta T_M$  is the temperature difference at zero sap flow, usually well approximated shortly before sunrise. Quantification of tree transpiration requires information on the area of the conducting tissue, i.e., the sapwood cross-sectional area,  $A_s$ , at the sensor positions. We estimated  $A_s$  from wood cores extracted at different azimuthal positions with an increment borer (300 mm; Suunto, Vantaa, Finland) at the end of the measurement campaign. Radial sapwood depth was estimated visually by differences in core transparency and microscopically as the section of unobstructed xylem vessels. According to Granier (1987) and Diawara et al. (1991), the error of this core method is less than 10%. Traditionally, sap flow ( $F$ ; g s<sup>-1</sup>) is calculated using the original equation of Granier (1985), assuming a constant  $J_s$  throughout the sapwood profile (Granier 1985, 1996b, Oren et al. 1996, Köstner et al. 1998, Phillips et al. 1999, Santiago et al. 2000, Oren and Pataki 2001):

Table 2. Sap flow measurements. Abbreviations: DBH = stem diameter at breast height;  $H$  = tree height;  $A_s$  = sapwood cross-sectional area; and  $F_{\text{mean}}$  and  $F_{\text{max}}$  = mean daily sums and maximum daily sap flow rates of the investigated trees, respectively. Standard deviations are in parentheses.

Genera/species	Family	DBH (cm)	$H$ (m)	$A_s$ (cm <sup>2</sup> )	$F_{\text{mean}}$ (kg day <sup>-1</sup> )	$F_{\text{max}}$ (g s <sup>-1</sup> )
<b>(a) Trees of the main study plot</b>						
<i>Ruagea cf. pubescens</i> H. Karst. <sup>1,2</sup>	Meliaceae	38.2	18.0	1036.7	81.6 (21.2)	2.90 (0.65)
<i>Aniba</i> sp.	Lauraceae	15.9	14.0	132.7	9.7 (3.6)	0.44 (0.16)
<i>Graffenrieda emarginata</i> Ruiz & Pav.	Melastomataceae	17.8	11.0	236.9	7.9 (5.4)	0.33 (0.23)
<i>Piper obtusifolium</i> L.	Piperaceae	11.1	12.0	96.4	4.5 (1.4)	0.20 (0.06)
<i>Psychotria tinctoria</i> Ruiz & Pav.	Rubiaceae	6.1	6.0	20.7	1.2 (0.4)	0.06 (0.01)
<i>Ocotea</i> sp.	Lauraceae	12.7	13.0	106.2	5.0 (2.5)	0.02 (0.13)
<i>Guarea</i> sp.	Meliaceae	42.0	18.0	1228.9	101.0 (11.8)	5.04 (1.78)
<i>Cecropia montana</i> Warb. ex Sthl.	Cecropiaceae	28.3	17.0	630.4	126.5 (27.8)	6.06 (3.21)
<i>Trichilia guianensis</i> <sup>2</sup> Klotzsch	Meliaceae	40.4	18.0	1166.3	120.9 (23.8)	4.15 (0.99)
<i>Aniba cf. muca</i> Ruiz & Pav.	Lauraceae	12.7	12.0	126.9	7.5 (4.7)	0.37 (0.24)
<b>(b) Trees of the pilot study plot</b>						
<i>Alzatea verticillata</i> Ruiz & Pav. <sup>1,2</sup>	Alzateaceae	45.0	13.5	1352.6	28.7 (13.7)	0.97 (0.33)
<i>Hyeronima</i> sp.	Euphorbiaceae	18.0	11.0	253.9	11.7 (3.4)	0.40 (0.08)
<i>Persea cf. cerulea</i> Ruiz & Pav.	Lauraceae	12.5	10.0	119.3	7.7 (2.8)	0.33 (0.09)
<i>Alzatea verticillata</i> (subcanopy)	Alzateaceae	20.2	11.0	313.9	5.6 (2.6)	0.19 (0.09)
<i>Schefflera morototoni</i>						
Maguire, Steierm. & Frodin	Araliaceae	13.1	9.0	132.4	2.4 (0.7)	0.08 (0.02)
<i>Ruagea cf. pubescens</i> H. Karst.	Meliaceae	22.0	10.0	379.6	21.7 (7.4)	0.89 (0.21)

<sup>1</sup> Sap flow sensors at two sapwood depths (0–20 mm, 20–40 mm).

<sup>2</sup> Sap flow sensors at two azimuthal positions of the stem.

$$F = J_s A_s \quad (4)$$

When applied to trees with high sapwood to stem cross-sectional area ratio, this assumption is questionable, and various studies have shown that radial variation of flux densities can be considerable (e.g., Phillips et al. 1996, James et al. 2002, Nadezhkina et al. 2002). In most of the tree species investigated,  $A_s$  reached about 80–95% of the total stem cross-sectional area (Table 2). Such high fractions of functional sapwood are surprising, but have been found in other tropical tree species as well (Goldstein et al. 1998, Phillips et al. 2001, T. Motzer, unpublished data from an Amazonian rain forest in southern Venezuela).

However, consistent with the results of Čermák et al. (1992), Lang (1999), Granier et al. (2000) and Lu et al. (2000), our data showed that  $J_s$  within the deeper sapwood (20–40 mm) is reduced to 85% of  $J_s$  within the outer xylem of the measured overstory trees of *A. verticillata* and *Ruagea pubescens* (Melastomataceae). Therefore, based on the measured flux profiles, two equations, one describing an exponential and the other a linear decay with sapwood depth, were applied (Motzer 2003, pp 213–216). Differences between these approaches were low (<5%), and, especially for the smaller trees comprising the majority of individuals, usually not significant. However, when comparing the modified approach with the traditional approach of constant  $J_s$  (Equation 4), discrepancies of up to 35% were apparent (for a detailed discussion, see Motzer 2003).

## Results

### Stomatal conductance and leaf transpiration

As predicted, leaf-to-leaf variability of  $g_s$  was considerable, even between adjacent leaves. Nevertheless,  $g_s$  was highest in the morning and tended to decline during the day, even under conditions of moderate atmospheric evaporative demand and generally sufficient soil water supply during the measurement period (soil water potential greater than –0.1 MPa).

Solar radiation and leaf-to-air vapor pressure deficit (VPD) are the major environmental determinants of  $g_s$  (e.g., Lange et al. 1976, Schulze and Küppers 1979, Turner et al. 1984, Meinzer et al. 1993), but are known to have offsetting effects on stomatal behavior (Meinzer et al. 1995, O'Brien et al. 2004). When mean  $g_s$  of the canopy trees *R. pubescens*, *Trichilia guianensis*, *Naucleopsis* sp. (Moraceae) and *Hedyosmum anisodorum* (Chloranthaceae) was plotted as a function of VPD alone,  $g_s$  appeared to decline with increasing VPD, although considerable scatter was evident in the relationship (Figure 1a). However, when photosynthetic photon flux (PPF) was normalized by VPD, a curvilinear dependence of stomatal opening on both PPF and VPD was evident (Figure 1b). High  $g_s$  reflected radiation-induced stomatal opening shortly after sunrise when PPF started to increase but VPD, and thus the VPD:PPF ratio, was low. On the other hand, low  $g_s$  coincided with diminishing sunlight in the late afternoon that induced stomatal closure when VPD, and thus the VPD:PPF ratio, was high. The exponential relationship between the VPD:PPF ratio and  $g_s$  was highly significant ( $r^2 = 0.52$ ,  $P < 0.0001$ ), and  $g_s$  can be described as:



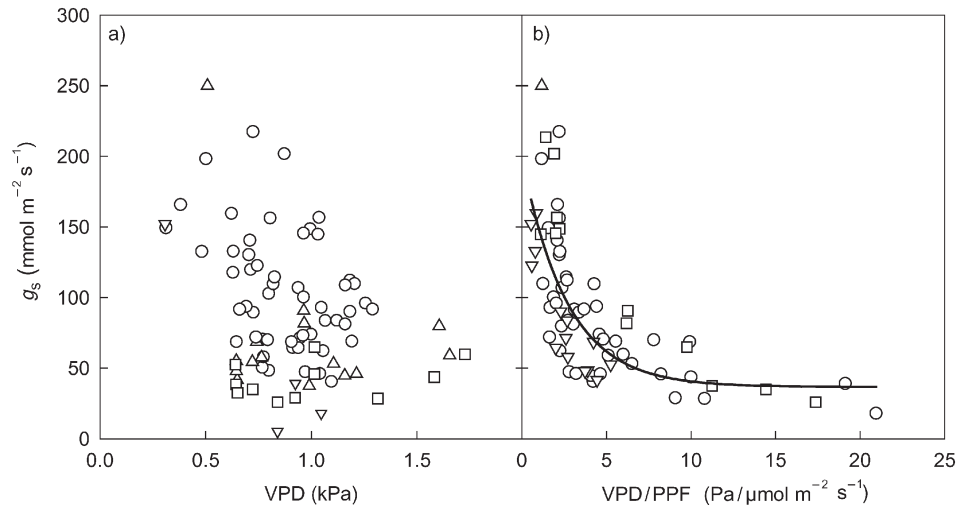


Figure 1. Relationships between stomatal conductance,  $g_s$ , and (a) vapor pressure deficit (VPD); and (b) VPD normalized by photosynthetic photon flux (PPF) for the canopy trees. Symbols:  $\circ$  = *Ruagea cf. pubescens*;  $\triangle$  = *Trichilia guianensis*;  $\square$  = *Naucleopsis sp.*; and  $\nabla$  = *Hedyosmum anisodorum*. Exponential relationship in (b):  $y = 36.73 + 162.48e^{-37.33x}$ ,  $r^2 = 0.52$ ,  $P < 0.0001$  (modified from Motzer 2003).

$$g_s = 36.73 + 162.48e^{-37.33VPD/PPF} \quad (5)$$

Similar dependencies of  $g_s$  on VPD and PPF were observed in the understory stratum (Figure 2). In this dim light zone, sunflecks likely caused sudden increases in  $g_s$  initiated a few seconds following the first light pulse and lasting for a few minutes, even in subsequent darkness (Zeiger et al. 1985, Küppers et al. 1999). The disjunct group of values in Figure 2 ( $\triangle$ ) is consistent with this type of post-illumination stomatal movement. The exponential relationship between PPF-normalized VPD and  $g_s$  was significant when the post-illumination values were ignored (Figure 2b, solid line), but it was less pronounced than in the canopy trees.

For all measured canopy trees, multiple regression analysis showed that 50–52% of the observed variance in  $g_s$  could be explained equally by PPF and VPD. In contrast, for the understory species, all measured meteorological variables explained

only 29% of the variance in  $g_s$ ; moreover, PPF accounted for only 1.2% of the variance, supporting the idea of post-illumination stomatal movements.

The atmospheric influence on  $g_s$  and stomatal control of  $E_1$  was substantially modified as a result of the wind, which affected the establishment of boundary layers on leaf and canopy surfaces, with their potential to decouple these surfaces from the atmospheric evaporative demand. To quantify possible influences of partial decoupling, dependencies of  $\Omega$  and  $E_1$  on  $g_s$  were evaluated (Figure 3). The decoupling coefficient increased with  $g_s$  in all species studied, regardless of their position within the forest canopy (Figures 3a and 3b). An initially linear relationship between  $g_s$  and  $\Omega$  became more scattered, and  $\Omega$  tended to saturate at higher  $g_s$ , resulting in a similar time course of  $E_1$ , because maximal values of  $g_s$  were usually observed at low leaf-to-air VPD. This situation prevailed under conditions of high atmospheric humidity and when a thick leaf

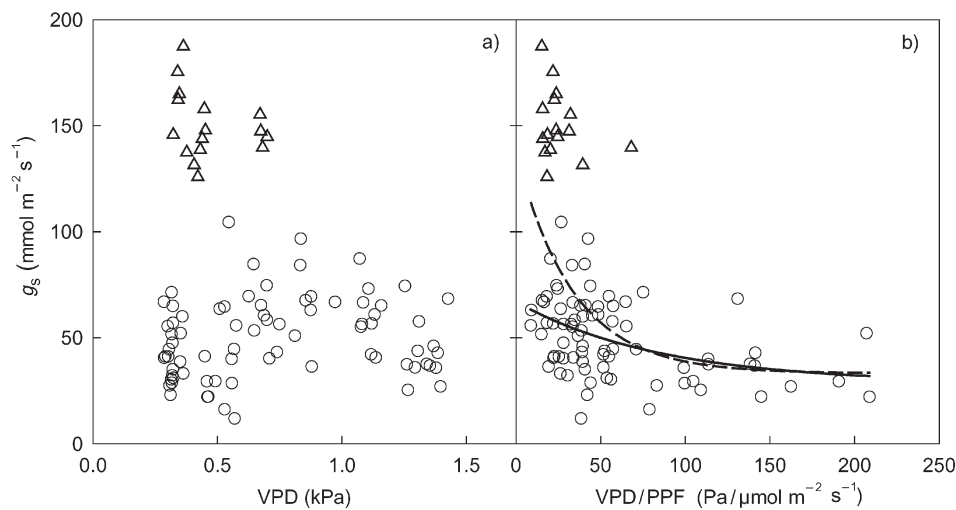


Figure 2. Relationships between stomatal conductance,  $g_s$ , and (a) vapor pressure deficit (VPD); and (b) VPD normalized by photosynthetic photon flux (PPF) for the understory individuals (all species listed in Table 1b). Symbols:  $\triangle$  = values assumed to have been obtained following a pulse of high irradiance (sunfleck); and  $\circ$  = values assumed to have been obtained without a prior pulse of high irradiance. Exponential

relationship disregarding post-illumination values (solid line) in (b):  $y = 28.58 + 38.43e^{-11.71x}$ ,  $r^2 = 0.19$ ,  $P = 0.0006$ ; dashed line is the exponential fit for all data.

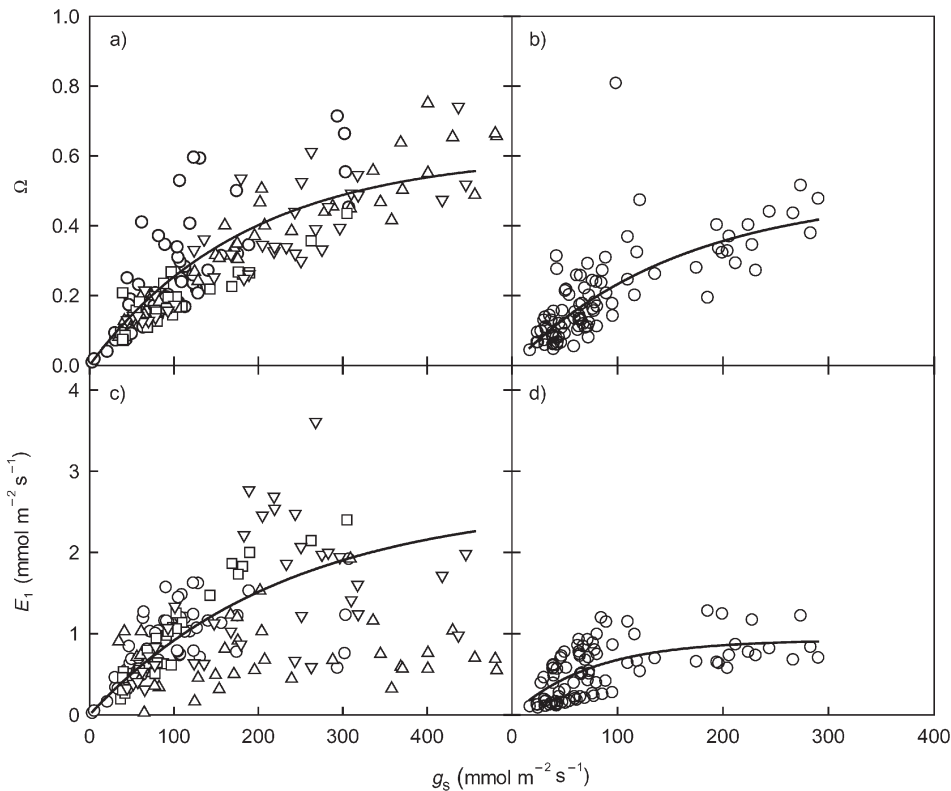


Figure 3. Relationships between stomatal conductance,  $g_s$ , and (a, b) the decoupling coefficient,  $\Omega$ ; and (c, d) leaf transpiration, for canopy trees (a, c) and understory trees (b, d). Symbols:  $\circ$  = *Ruagea cf. pubescens*;  $\triangle$  = *Trichilia guianensis*;  $\square$  = *Naucleopsis sp.*;  $\nabla$  = *Hedyosmum anisodorum*; and  $\circ$  = understory trees (b, d). Values are means of 4–10 leaves representing a single measurement run. Exponential fits ( $P < 0.001$ ): (a)  $r^2 = 0.63$ ; (b)  $r^2 = 0.69$  (disregarding outlier); (c)  $r^2 = 0.53$ ; and (d)  $r^2 = 0.4$ .

boundary layer (low  $g_s$ ) decoupled the leaf surface from the atmospheric evaporative demand. However, despite high  $g_s$ , transpiration was inhibited (Figure 3c) by low vapor pressure gradients characteristic of decoupled conditions (Figure 3a:  $\Omega \rightarrow 1$ ). Greater decoupling usually occurred in the morning when low wind speed promoted the establishment of thick leaf and canopy boundary layers. With increasing daily turbulence, atmospheric coupling increased as a result of the diminishing boundary layer, and the enhanced transpirational water loss, even at constant VPD, led to stomatal restriction. Decoupling coefficient values, typically ranging from 0.25 to 0.43 for the canopy trees, indicated relatively good atmospheric coupling during daytime, but deviations from the mean were large (Table 1). Decoupling coefficient values of the understory trees was within the same range or lower ( $< 0.3$ ).

Mean  $g_s$  of the dominant canopy trees studied (*R. pubescens*, *T. guianensis*, *Naucleopsis sp.*, *H. anisodorum*) was  $165 \text{ mmol m}^{-2} \text{ s}^{-1}$ . The highest values of  $g_s$  ( $> 600 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) were observed in *H. anisodorum* and *T. guianensis*. Although maximum  $g_s$  of understory individuals exceeded  $300 \text{ mmol m}^{-2} \text{ s}^{-1}$ , mean  $g_s$  for the understory was about  $90 \text{ mmol m}^{-2} \text{ s}^{-1}$  (Table 1).

#### Diurnal sap flow pattern and comparison of species

Typical diurnal courses of  $J_s$  representative of days with different weather conditions are shown in Figure 4. Daily variations in  $J_s$  appeared to be mainly associated with variations in VPD and PPF. After sunrise,  $J_s$  of the upper-canopy trees lagged behind increasing radiation and VPD by up to 1 h (Figure 4b). In

individuals of the forest interior (Figure 4c), this time lag was even greater, and their  $J_s$  dropped earlier in the evening, resulting in a contracted time course of  $J_s$ . The more gradual decline in  $J_s$  after sunset could be attributed to the recharge of water-storing tissues (Goldstein et al. 1998), causing a delay in the return to zero flow until early morning. Concomitant dendrometric measurements of diurnal variations in stem and twig diameters revealed that tissue water storage contributed to daily  $F$  only during the evening, and the nocturnal recharge phase was responsible for the initial time lag after sunrise (0700–0900 h, up to 1000 h) (Motzer 2003, D. Schmitt, unpublished observations). Except for these periods, dendrometric evidence, as well as cross-correlation analysis performed on  $J_s$  and VPD, proved the absence of a time lag during the rest of the day. Correlation coefficients were maximal at offsets of  $\Delta t = -5 \text{ min}$  to  $\Delta t = 0 \text{ min}$  ( $R = 0.61–0.83$ ).

Quantitatively, differences in  $J_s$  between trees were small, except for *Cecropia montana* (Cecropiaceae), which is considered to be a light-demanding, fast-growing, late-stage pioneer species (Berg and Franco 1992). Its  $J_s$  exceeded  $100 \text{ g m}^{-2} \text{ s}^{-1}$  under favorable conditions, but because of its relatively small DBH, mean whole-plant water consumption was only slightly higher ( $125 \text{ kg day}^{-1}$ ) than for other overstory trees (see Table 2) where long-term midday mean (1200–1400 h)  $J_s$  was usually within the range of  $40–60 \text{ g m}^{-2} \text{ s}^{-1}$ . Generally, between tree differences were more pronounced for  $F$  than for  $J_s$ , because taller trees possess both a higher  $J_s$  and a larger  $As$ . Sap flow increased dramatically with tree height and with DBH (Figure 5), which is often a reliable indicator of functional sapwood area (Meinzer et al. 2001, Motzer 2003, Wie-

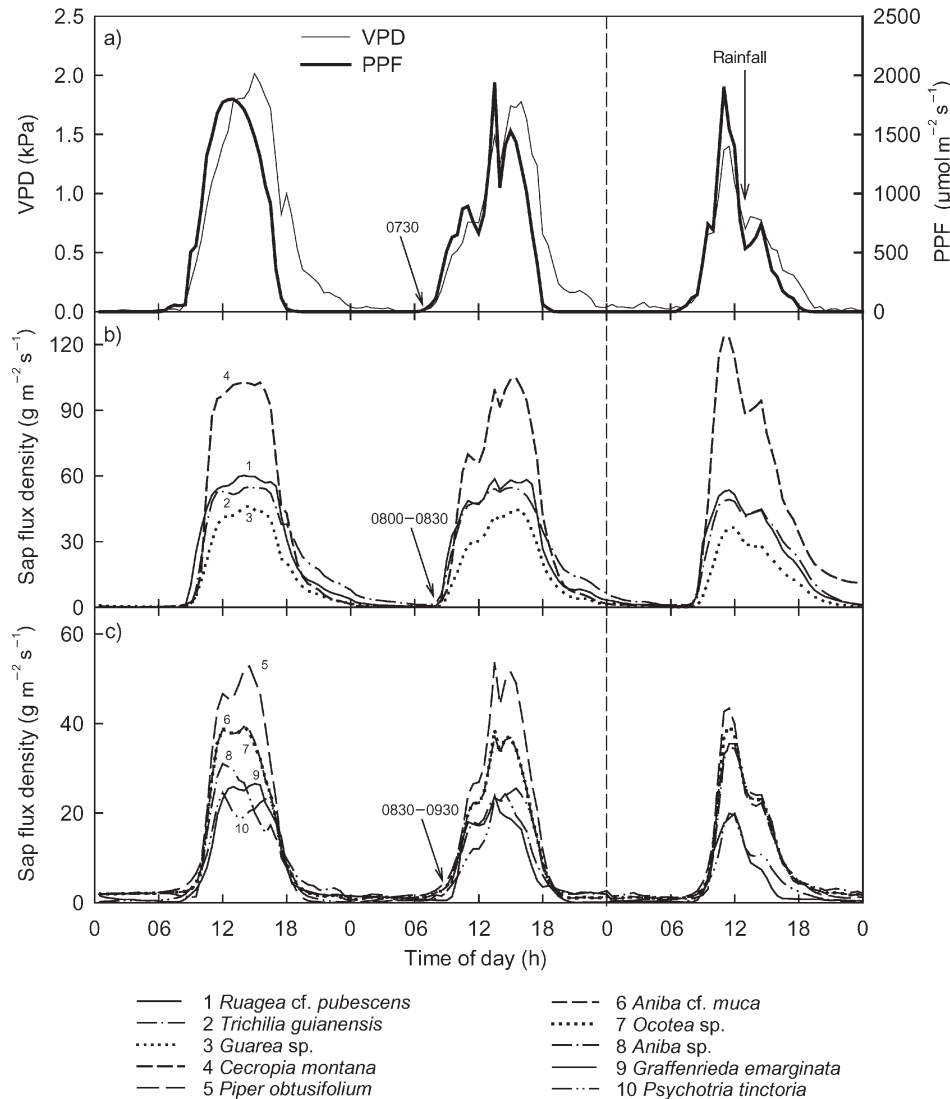


Figure 4. Daily courses of sap flux density of the (b) over-story trees and the (c) mid- and subcanopy trees compared with (a) daily courses of vapor pressure deficit (VPD) and photosynthetic photon flux (PPF), on a bright day (left, September 5, 2000), a cloudy day (center, September 6, 2000) and an overcast day with rain (right, September 8, 2000). Arrows indicate the time of the day when curves start to rise in the morning. Note the different y-axis scales in (b) and (c) (modified from Motzer 2003).

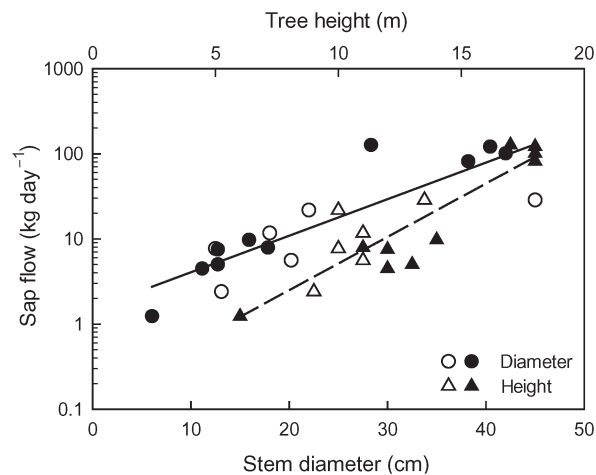


Figure 5. Daily sap flow totals of the investigated trees as a function of tree height (●) and stem diameter (▲). Open symbols = trees of the pilot plot. Sap flow is plotted on a log-scale to linearize the relationship to stem diameter ( $r^2 = 0.75$ ,  $P < 0.001$ ) and height (dashed line,  $r^2 = 0.8$ ,  $P < 0.001$ ).

mann et al. 2004). Daily totals of  $F$  ranged from  $80\text{--}120 \text{ kg day}^{-1}$  to  $165 \text{ kg day}^{-1}$  for dominant-canopy trees, where transpiration of intermediate and suppressed mid- and subcanopy trees, with at least partly shaded crowns, was an order of magnitude lower ( $1.3\text{--}9.7 \text{ kg day}^{-1}$  (maximum up to  $18.9$ ); Figure 5, see also Table 2).

*Responses of tree transpiration to the atmospheric environment*

Whole-tree transpiration (sap flow measurements) responded more distinctly to light than  $E_1$  (and  $g_s$ ). Daily totals of  $J_s$  were linearly correlated with PPF sums ( $r^2 = 0.61\text{--}0.71$ ) for all investigated trees (Figure 6). Furthermore, multiple regression analysis with meteorological parameters as independent variables and sap flux as the dependent variable revealed that 56–71% of the variance in  $J_s$  was explained by daily PPF sums. Addition of other meteorological parameters (VPD, wind speed, air temperature) enhanced the explainable variance by no more than 10%, mainly attributable to VPD.

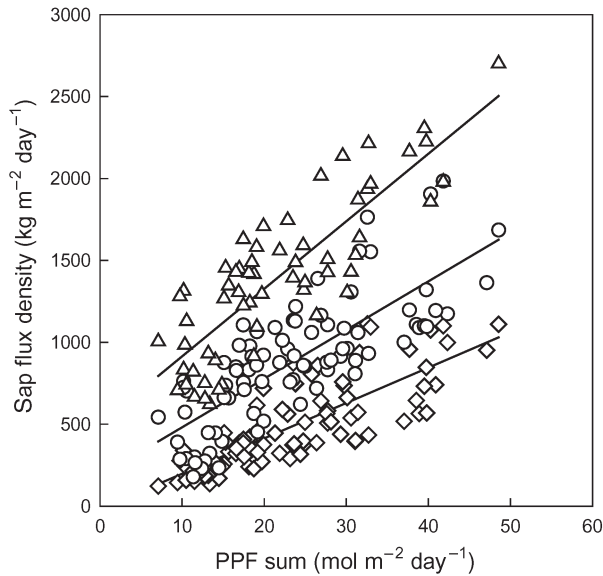


Figure 6. Sap flux density in relation to daily photosynthetic photon flux (PPF) sums. Symbols:  $\Delta$  = *Trichilia guianensis*;  $\circ$  = *Ruagea cf. pubescens*; and  $\diamond$  = *Aniba cf. muca*. Linear correlations are significant for all trees at  $P < 0.001$ ;  $r^2$  is 0.71, 0.61, 0.65 for *T. guianensis*, *R. pubescens* and *A. muca*, respectively.

In contrast, VPD appeared to be a main driver of tree transpiration during the day. In Figure 7,  $J_s$  of *R. pubescens* (overstory), *A. muca* (midcanopy) and *Psychotria tinctoria* (subcanopy) is plotted against VPD, subdivided into four radiation classes. When daytime VPD exceeded 1 kPa, PPF was usually above  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . On mostly sunny days,  $J_s$  initially increased with VPD in a nearly linear fashion when VPD was less than 1 kPa. Under conditions of greater atmospheric evaporative demand (VPD > 1–1.2 kPa),  $J_s$  became relatively insensitive to variation in PPF or VPD, resulting in asymptotic relationships (0600 to 1500 h) with  $r^2$  of 0.91 for *R. pubescens* and *A. muca*, 0.89 for *P. tinctoria* and 0.7–0.9 for all other trees (not shown,  $P < 0.0001$ ). The hystereses in Figure 7 were attributable to the gradual decline in  $g_s$  during the day, which led to decreasing  $J_s$ , irrespective of high evaporative demand in the afternoon.

## Discussion

Our results provide basic quantitative information and insights into processes controlling tree transpiration and stomatal behavior of TMF trees at their natural sites. Our results show that diurnal radiation determines the general stomatal status, whereas variable VPD accounts for intermediate coordination of stomatal movements throughout the day, thereby limiting the risk of severe water deficits. Atmospheric coupling of stomata was good and  $\Omega$  values (0.25 to 0.43) were considerably lower than those reported by Meinzer et al. (1995) ( $\Omega \sim 0.75$ ) or Roberts et al. (1990) ( $\Omega \sim 0.78$  for understory trees) for lowland tropical forest trees, but they are within the same range of values measured by Kumagai et al. (2004) in a

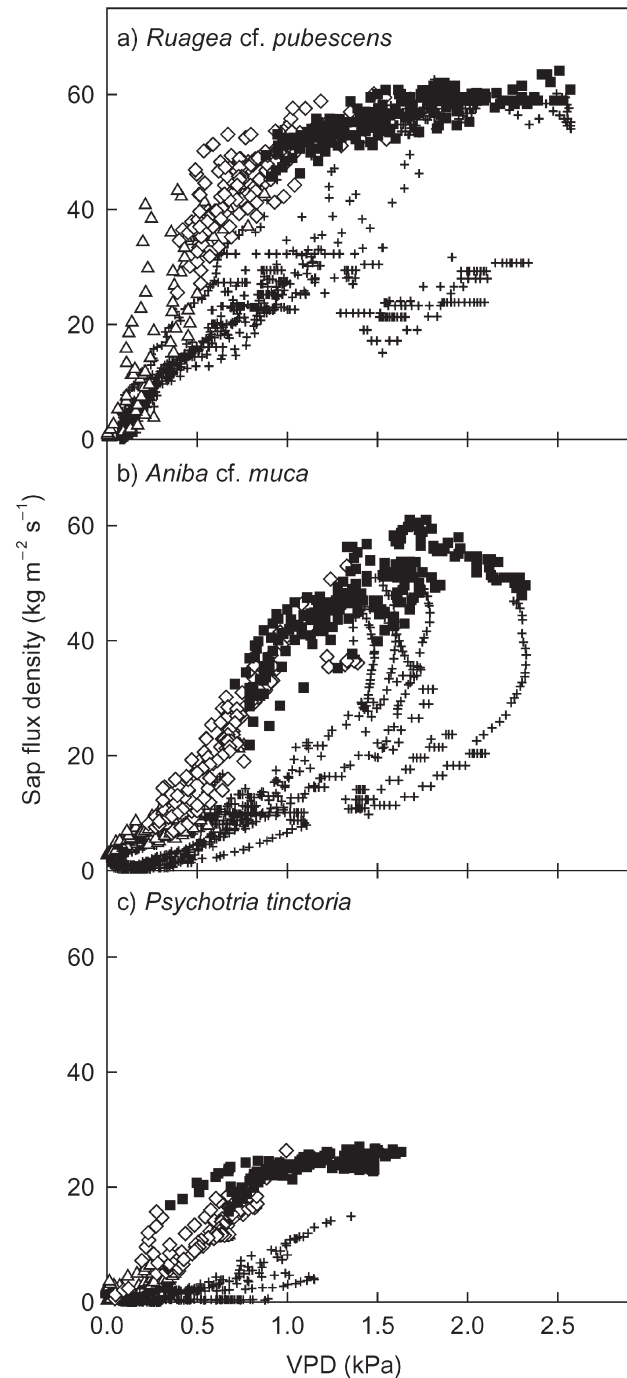


Figure 7. Sap flux density in relation to vapor pressure deficit (VPD) measured at a similar height in the respective tree crowns: (a) overstory tree *Ruagea cf. pubescens*, (b) midcanopy tree *Aniba cf. muca*, (c) subcanopy tree *Psychotria tinctoria*. Symbols indicate differences in photosynthetic photon flux (PPF) over the previous 1-h period:  $\Delta$  = 50–600;  $\diamond$  = 600–1200;  $\blacksquare$  = > 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (data from 0600 to 1500 h); and + = all data collected later than 1500 h (modified from Motzer 2003).

dipterocarp forest. To our knowledge, there are at present no other data available for similar tropical montane environments.



Similarly, little information is available on maximum stomatal conductance,  $g_{\max}$ , in TMF trees, which may be considered an estimate of potential maximum  $E_1$  and maximum net photosynthesis. However,  $g_{\max}$  ( $233 \pm 93 \text{ mmol m}^{-2} \text{ s}^{-1}$ ) of our study trees was well within the range of mean  $g_{\max}$  of  $249 \pm 133 \text{ mmol m}^{-2} \text{ s}^{-1}$  for humid tropical forests in general, as compiled by Körner (1995) in a global comparison. Aylett (1985) reported mean  $g_{\max}$  values of 278, 305 and  $178 \text{ mmol m}^{-2} \text{ s}^{-1}$  for two tall canopy trees (*Clethra occidentalis* (L.) Kuntze, *Cyrilla racemiflora* L.) and the subcanopy tree *Hedyosmum arborescens* Sw., respectively, all from an upper montane rain forest in Jamaica. Santiago et al. (2000) observed high variations in  $g_{\max}$  and  $g_s$  of *Metrosideros polymorpha* Gaud. trees in a Hawaiian montane cloud forest, and showed that mean  $g_s$  decreased linearly with increasing tree height from  $340 \text{ mmol m}^{-2} \text{ s}^{-1}$  (0.9 m) to  $56 \text{ mmol m}^{-2} \text{ s}^{-1}$  (6.4 m).

It is well documented (e.g., Schulze and Küppers 1979) that stomata regulate  $E_1$  at increasing VPD such that a maximum value of  $E_1$  is normally reached. This control carries over from the leaf to the canopy level, and the observed tendency of  $J_s$  to saturate at high VPDs ( $> 1\text{--}1.2 \text{ kPa}$ ; Figure 7) provides evidence for strong stomatal limitation of transpiration. Such an upper limit on transpiration has also been reported for temperate (e.g., Hogg and Hurdle 1997, Zhang et al. 1997, Oren and Pataki 2001, Pataki and Oren 2003) and tropical lowland forest trees (Meinzer et al. 1993, 1995, Granier et al. 1996b, Oren et al. 1996, Anhuf et al. 1999).

Daily totals of  $F$  of the measured canopy trees were usually well below  $150 \text{ kg day}^{-1}$ , depending on tree crown status and meteorological conditions. But when comparing sap flow rates of other tropical rain forest trees, large quantitative differences became evident, even in comparable habitats or species. Sap flow rates of large *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels trees in a Panamanian lowland forest were reported to be  $380 \text{ kg day}^{-1}$  (DBH = 102 cm; Andrade et al. 1998) and up to  $750 \text{ kg day}^{-1}$  (DBH = 98 cm; James et al. 2002). Granier et al. (1996b) measured  $F$  of  $250\text{--}300 \text{ kg day}^{-1}$  in different trees (DBH = 45–57 cm) in French Guiana. On the other hand, Oren et al. (1996) and Anhuf et al. (1999) reported mean transpiration rates of only  $50\text{--}60 \text{ kg day}^{-1}$  for dominant canopy trees (DBH = 55–100 cm) in the Peruvian and Venezuelan Amazon, respectively. Similarly, in montane environments, the few existing data indicate extraordinarily high variability in tree transpiration rates, ranging from  $5\text{--}35 \text{ kg day}^{-1}$  (Santiago et al. 2000) and  $10\text{--}110 \text{ kg day}^{-1}$  (Zotz et al. 1998) up to  $372 \text{ kg day}^{-1}$  (Kline et al. 1970).

Comparatively low transpiration rates of TMF trees may result from hydraulic insufficiency (Cavelier 1996), anaerobic toxic soil conditions or low nutrient availability (Bruijnzeel and Proctor 1995, Cavelier et al. 2000). At our study site, the last two explanations seem unlikely based on the pedochemical analysis of Wilcke et al. (2001), and the finding that maximum  $J_s$  ( $> 65 \text{ g m}^{-2} \text{ s}^{-1}$ ) was as high as values reported for lowland forests does not support the hypothesis of Cavelier (1996). Our results indicate that tree transpiration was repressed chiefly by the frequent cloud cover and high atmospheric hu-

midity, as suggested by Steinhardt (1979) and Santiago et al. (2000). In agreement with Bruijnzeel (1990), our data do not support the hypothesis of a general decrease with altitude in  $g_s$ ,  $g_{\max}$  and potential transpiration rates (at either the leaf or the tree level).

Of particular importance for further scaling up and modeling of stand transpiration is the finding that differences in transpirational behavior were more pronounced between trees differing in DBH and crown area than between different species (Motzer et al. 2005). This is in agreement with the results of Granier et al. (1996b), Andrade et al. (1998) and Meinzer et al. (2001), who concluded that crown status (e.g., large, (co)dominant or small, suppressed), rather than species-specific influences, is the major element determining sap flow rates. However, when scaling to the stand, differing physiological traits of the measured species also have to be considered. Pioneer tree species and shrubs usually possess a high-capacity water transport system allowing high  $J_s$  values, e.g., *C. montana* in our study (see also Küppers 1984, Berg and Franco 1992, Tyree et al. 1998), and old trees often have lower transpiration rates (Tyree and Zimmerman 2002), as did the upper-canopy tree of *A. verticillata* at the pilot plot (see Table 2).

High variation in the few available data demonstrates that further field research is necessary both to develop a coherent picture of the water relations of tropical trees in various habitats and to parameterize regional water flux models for assessing possible consequences of human perturbations or global climate change on the functioning of tropical forest ecosystems.

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