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Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties

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Abstract Environmental and physiological regulation of transpiration were examined in several gap-colonizing shrub and tree species during two consecutive dry seasons in a moist, lowland tropical forest on Barro Colorado Island, Panama. Whole plant transpiration, stomatal and total vapor phase (stomatal + boundary layer) conductance, plant water potential and environmental variables were measured concurrently. This allowed control of transpiration (E) to be partitioned quantitatively between stomatal (g_s) and boundary layer (g_b) conductance and permitted the impact of individual environmental and physiological variables on stomatal behavior and E to be assessed. Wind speed in treefall gap sites was often below the 0.25 m s^{-1} stalling speed of the anemometer used and was rarely above 0.5 m s^{-1}, resulting in uniformly low g_b (c. 200–300 mmol m^{-2} s^{-1}) among all species studied regardless of leaf size. Stomatal conductance was typically equal to or somewhat greater than g_b. This strongly decoupled E from control by stomata, so that in *Miconia argentea* a 10% change in g_s when g_s was near its mean value was predicted to yield only a 2.5% change in E. Porometric estimates of E, obtained as the product of g_s and the leaf-bulk air vapor pressure difference (VPD) without taking g_b into account, were up to 300% higher than actual E determined from sap flow measurements. Porometry was thus inadequate as a means of assessing the physiological consequences of stomatal behavior in different gap colonizing species. Stomatal responses to humidity strongly limited the increase in E with increasing evaporative demand. Stomata of all species studied appeared to respond to increasing evaporative demand in the same manner when the leaf surface was selected as the reference point for determination of external vapor pressure and when simultaneous variation of light and leaf-air VPD was taken into account. This result suggests that contrasting stomatal responses to similar leaf-bulk air VPD may be governed as much by the external boundary layer as by intrinsic physiological differences among species. Both E and g_s initially increased sharply with increasing leaf area-specific total hydraulic conductance of the soil/root/leaf pathway (G_t), becoming asymptotic at higher values of G_t. For both E and g_s a unique relationship appeared to describe the response of all species to variations in G_t. The relatively weak correlation observed between g_s and midday leaf water potential suggested that stomatal adjustment to variations in water availability coordinated E with water transport efficiency rather than bulk leaf water status.

Key words Tropical forest · Transpiration · Stomata
Boundary layer · Hydraulic conductance

Introduction

Many of the moist, lowland tropical forests of Central America and northern South America experience a pronounced, 3–4 month dry season. Treefall gaps in these forests are rapidly colonized by fast-growing, high-light-requiring pioneer species (Foster and Brokaw 1982). Both gap-colonizing species and shade-tolerant understory shrubs typically retain their leaves throughout the

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dry season (Croat 1978; Wright and Cornejo 1990; Wright 1991). Although responses to seasonal drought have been described for a number of understory shrub species (e.g., Mulkey et al. 1991; Wright 1991; Wright et al. 1992) there have been few studies of drought responses in gap-colonizing species (e.g., Fanjul and Barradas 1985; Reekie and Wayne 1992). The available data suggest that in understory shrubs rates of water use are generally low and water use is greatly restricted during the dry season (Mulkey et al. 1992, 1993). It appears that stomatal conductance is substantially higher in gap-colonizing than in understory species even when both co-occur in gaps. This implies that gap colonizers are able to sustain greater rates of water use and evaporative cooling throughout the dry season. In all of the studies cited above, transpiration rates have been inferred from porometric measurements of stomatal conductance and not measured directly. To our knowledge there are no reports of absolute rates of water use in either gap-colonizing or shade-tolerant understory species determined with more direct methods than porometry and leaf gas exchange.

Several features of treefall gap species and of the gap microenvironment suggest that transpiration in these species may be appreciably decoupled from regulation by stomata. Porometric measurements of stomatal behavior in these species may thus be unreliable predictors of the behavior of transpiration. The extent to which stomatal movements control transpiration is largely a function of the ratio of stomatal conductance to the conductance of the boundary layers surrounding each leaf and the entire canopy. Stomatal control of transpiration is strong only when boundary layer conductance is high in relation to stomatal conductance (Jarvis and McNaughton 1986). If boundary layer conductance is low, transpiration from the leaves will promote local humidification of the air surrounding the leaves, uncoupling the vapor pressure at the leaf surface from that in the bulk air. In gap-colonizing species both the relatively large leaf size and the rapid attenuation of wind down through the canopy as the forest floor is approached would be expected to result in low boundary layer conductance. For example, Roberts et al. (1990) estimated boundary layer conductance to be approximately 5 times higher in the upper canopy than near the forest floor in an Amazonian forest. Even in leaves located in the mid to upper canopy, large leaf size, close spacing, and dense, compact crown architecture may reduce boundary layer conductance (Grace et al. 1980) thereby diminishing the impact of stomatal movements on transpiration (Meinzer et al. 1993). Other features of the treefall gap microenvironment may make characterization of the role of stomata in regulating transpiration of colonizing species difficult. Simultaneous variation and rapid changes in major environmental factors known to exert opposing influences on stomatal conductance may partially obscure stomatal responses to individual environmental factors.

In this paper we report on patterns of transpiration and stomatal behavior in several gap colonizing species observed during two successive dry seasons in a moist, lowland forest on Barro Colorado Island, Panama. The species selected were known to have relatively high rates of stomatal conductance and therefore potentially high transpiration rates during the dry season. Our objectives were to integrate concurrent measurements at the single-leaf and crown levels in order to evaluate the effectiveness of stomatal movements in controlling transpiration and to assess the relative roles of the boundary layer and individual environmental and physiological variables in regulating stomatal behavior and transpiration.

Materials and methods

Field site and plant material

The study was carried out in a lowland tropical moist forest on Barro Colorado Island (BCI), Panama (9° 10'N, 79° 51'W). Mean annual precipitation is 2,600 mm. There is a pronounced dry season from mid-December through April during which only about 5% of the total annual precipitation falls. During this period the water potential in the upper 20 cm of the soil profile can fall to –2 MPa (Becker et al 1988). Measurements were carried out in two treefall gap sites during February and March 1991 and two different gap sites during February and March 1992. Gap size ranged from c. 25 to 100 m^2. Rainfall for January–March 1991 was 218 mm and only 46 mm for January–March 1992.

Five gap-colonizing evergreen tree and shrub species were selected for study on the basis of their abundance and accessibility (Table 1). The experimental plants were approximately 1–2.5 m tall to allow measurements to be made without erecting ladders or towers. *Miconia argentea* (SW.) DC., Melastomataceae, was the most abundant of the five species and occurred in each site. It has large, opposite leaves up to 38 cm long and 27 cm wide. Adult individuals attain a maximum height of about 15 m. *Palicourea guianensis* Aubl., Rubiaceae, a shrub or small tree attaining a maximum height of c. 3.5 m, also occurred in each site but was less abundant than *M. argentea*. The individuals studied were 1–2 m tall shrubs with leaves 12–25 cm long and 6–13 cm wide. *Cecropia obtusifolia* Bertol. and *C. insignis* Liebm., Moraceae, are gap pioneer trees which grow rapidly without branching as juveniles, retaining only a terminal set of large, palmate leaves. The individuals studied had leaves c. 30 cm across. *Coccoloba manzanillensis* Beurl., Polygonaceae, a small tree usually less than 30 m tall, had large, corrugated leaves c. 30 cm long and 20 cm wide and was present at only one site.

Transpiration and hydraulic conductance

Transpiration (E) was measured as mass flow through entire plants using a heat balance method as described by Baker and Van Bavel (1987). Sap flow gauges (Models SGA-10, SGB-13, SGB-16, Dy-

Table 1 Maximum stomatal conductance and average midday transpiration (1000–1400 hours) for gap-colonizing species on Barro Colorado Island, Panama during the dry seasons of 1991 and 1992

Species	Maximum g_s (mmol m^{-2} s^{-1})		Midday E (mmol m^{-2} s^{-1})	
	1991	1992	1991	1992
Miconia argentea	382	218	1.41	1.05
Palicourea guianensis	194	38	1.48	0.14
Cecropia obtusifolia	212	133	1.06	0.98
Cecropia insignis	–	208	–	1.45
Coccoloba manzanillensis	–	222	–	1.04

namax Inc., Houston, Tex., USA) consisting of a heating element, a thermopile and individual thermocouples were attached to main stems approximately 30–50 cm above the soil surface. The gauges and adjacent portions of the stem were wrapped with foam insulation in addition to that supplied by the manufacturer and the entire assembly was enclosed in an outer layer of aluminum foil in order to minimize spurious temperature gradients caused by radiant heating of the stem (Gutiérrez et al. 1994). The heating elements were operated at constant power and the radial and longitudinal heat fluxes were evaluated with the thermopile and thermocouples, respectively. A datalogger (CR21X, Campbell Scientific Corp., Logan, Utah, USA) equipped with a 32-channel multiplexer (AM 416, Campbell Scientific) permitted several gauges to be operated simultaneously. Data were recorded continuously and 20-min averages were stored in a solid state storage module (SM 196, Campbell Scientific). The sheath conductance for each gauge, a proportionality constant relating thermopile output to the radial heat loss at zero flow, was determined from the average values of sheath conductance calculated in the datalogger program between 0300 and 0600 hours local time when transpiration was assumed to be zero. Gauges were typically operated for several consecutive days at each site. Upon completion of the measurements, all leaves were removed from the plants for determination of their area in an area meter (model 3100, LI-COR, Inc., Lincoln, Neb., USA). Total leaf area was typically 0.4–1.0 m^2. All values of E reported here are on a unit leaf area basis.

The heat balance method has been applied sucessfully to woody species growing under field conditions (e.g., Steinberg et al. 1989, 1990; Heilmann and Ham 1990; Gutiérrez et al. 1994). Nevertheless, we deemed it desirable to evaluate the method's performance under the conditions of our study. Individuals of *M. argentea, C. obtusifolia* and *P. guianensis* fitted with sap flow gauges were decapitated and the bases of their stems installed in potometers. Subsequent, simultaneous measurements of sap flow and water movement through the potometers were within 10% of each other and not significantly different from a 1:1 relationship over the entire range of sap flow measured (0–50 g h^{-1}).

The leaf area-specific total hydraulic conductance of the soil/root/leaf pathway (G_t) for plants fitted with sap flow gauges was determined as

$$G_t = \frac{E}{\Delta\Psi}$$

where $\Delta\Psi$ is the difference between soil water potential and midday leaf water potential and E is the average transpiration rate at the time midday leaf water potential was determined. Predawn leaf water potential was used as an approximation of soil water potential. Midday leaf water potential was measured between 1200 and 1400 hours when E was typically maximal. Water potential was measured psychrometrically in small leaf discs in order to avoid excessive defoliation of the study plants which had relatively few leaves. Small leaf strips were rapidly excised, sealed inside resealable plastic bags and held in darkness during transport to the laboratory. Processing of leaf samples in the laboratory began within 15 min of their excision in the field. Two replicate leaf discs were rapidly obtained from each leaf strip with a cork borer and sealed inside psychrometer chambers (83 series, JRD Merrill Specialty Equipment, Logan, Utah). The psychrometer chamber assemblies were placed in a water bath inside an insulated box and allowed to equilibrate for 4–6 h. Previous measurements on leaf discs from the same species had shown that 2–3 h were typically required for equilibration and stable water potential readings. Measurements were taken with a 12-channel digital psychrometer meter (85 series, JRD Merrill Specialty Equipment) in the psychrometric mode. The psychrometers were calibrated regularly with salt solutions of known water potential.

Micrometeorological measurements

Data were recorded continuously with a second datalogger and a solid state storage module identical to those used for the sap flow measurements described above. Photosynthetic photon flux density (PPFD) was measured with a quantum sensor (LI-190SB, LI-COR, Inc., Lincoln, Neb., USA) positioned horizontally. Relative humidity and temperature were measured with shielded sensors (HMP35C, Campbell Scientific) installed at approximately 1.5 m height. Ambient vapor pressure was subsequently calculated from the relative humidity and temperature data. Wind speed was monitored with a high-sensitivity, 0.25 m s^{-1} stalling speed cup anemometer (Model 2030, Qualimetrics, Inc., Sacramento, Calif.) installed at 1.5 m. All sensors were mounted at a location approximately equidistant from the plants fitted with sap flow gauges. Leaf temperature of the plants fitted with sap flow gauges was determined with fine wire (0.08 mm) copper constantan thermocouples. One thermojunction was affixed to the abaxial surface of each of five leaves on each of the plants fitted with sap flow gauges. Thermojunctions were constructed to allow approximately 3 cm of constantan wire to extend beyond the junction. The leaf blade was pierced with a small needle to permit the constantan wire to be inserted through the leaf from the adaxial side and pulled until the thermocouple junction and about 2 cm of the copper-constantan duplex wire appeared below the abaxial surface. The leaf was pierced again at a point about 3 cm away from the original perforation and the constantan wire was pushed through until about 2 cm appeared above the adaxial surface. The thermojunction was brought into contact with the abaxial surface by pulling on the constantan and duplex wires until they were relatively taut. Each wire was then secured to the adaxial surface with a small piece of water-resistant adhesive tape. This attachment procedure did not encumber the thermojunction itself, thereby avoiding undue interference with the leaf energy balance near the thermojunction. The vapor pressure difference between the leaf interior and the bulk air (VPD_a) was calculated using saturation vapor pressure at leaf temperature and the ambient vapor pressure determined as described above. Crown conductance (g_c; mol m^{-2} s^{-1}) was calculated as

$$g_c = \frac{EP}{VPD_a}$$

where P is atmospheric pressure. All values of g_c are expressed on a unit leaf area basis. Crown conductance as defined here includes a stomatal component, and boundary layer components whose magnitude is determined both by leaf dimensions and by attenuation of wind by the surrounding vegetation. It can therefore be regarded as partially analogous to a canopy conductance, even though the latter is traditionally expressed on a unit ground area basis (Meinzer et al. 1993). Boundary layer conductance (g_b) was calculated from g_c and g_s as

$$g_b = 1/(1/g_c - 1/g_s)$$

Stomatal control of transpiration

Stomatal conductance was measured with a steady-state porometer (model 1600, LI-COR, Inc.) in four to five premarked leaves on each of the plants fitted with sap flow gauges. For *Cecropia* spp. and *M. argentea* the leaves on which g_s was determined made up c. 30–50% of the total leaf area per plant. Typically, four to six complete sets of measurements were obtained between 0800 and 1600 hours during each of 2–4 days of measurements at a given site. All values of g_s reported are of the abaxial leaf surface of these hypostomatous species.

A dimensionless decoupling coefficient, Ω, ranging from 0 to 1 was calculated to describe the extent to which leaf and canopy boundary layers decoupled the vapor pressure at the leaf surface from that in the bulk air, impeding stomatal control of transpiration. The procedure of Jarvis and McNaughton (1986), with a modification proposed by Martin (1989) that takes the radiative coupling between leaves and the atmosphere into account, was used to calculate Ω as

$$\Omega = \frac{\varepsilon + 2 + g_r / g_b}{\varepsilon + 2 + (g_b + g_r) / g_s + g_r / g_b}$$

where ε is the ratio of the increase of latent heat content to increase of sensible heat content of saturated air and g_r is a long-wave radiative transfer 'conductance' of the canopy.

This definition of Ω follows that of McNaughton and Jarvis (1991) for a hypostomatous leaf symmetrical with respect to g_b. Stomatal control of transpiration grows progressively weaker as Ω approaches 1.0 because the vapor pressure at the leaf surface becomes increasingly decoupled from that in the bulk air. The leaf surface was used as an additional external reference point for characterizing stomatal responses to humidity and their consequences for transpiration. The leaf-to-air vapor pressure diffference at the leaf surface (VPD_s, kPa) was estimated as

$$VPD_s = EP/g_s$$

Results

Maximum rates of stomatal conductance and average midday transpiration varied considerably among species and years (Table 1). In the three species for which 2 years of data were available both g_s and E were substantially lower in the dry season of 1992, during which only 46 mm of precipitation were recorded between January and March. The relative reduction in g_s and E in 1992 compared to 1991 were much greater in *P. guianensis* than in either *M. argentea* or *C. obtusifolia*. The ranking of species according to their average transpiration rates was not always consistent with their ranking according to maximum g_s. This was probably attributable to the tendency for maximum g_s to occur when evaporative demand was lowest and to differences in the stomatal decoupling coefficienct (Ω) among species (see below).

Representative daily courses of transpiration, total vapor phase conductance and environmental variables for *M. argentea* plants in gap sites 3 and 4 during the dry season of 1992 are presented in Fig. 1. The two sites differed markedly with respect to prevailing PPFD and wind speed. In site 3, PPFD was below 200 μmol m^{-2} s^{-1} throughout most of the day except for a 2-h period between 1200 and 1400 hours during which maximum values exceeded 1000 μmol m^{-2} s^{-1}. Wind speed was nearly always below the 0.25 m s^{-1} stalling speed of the anemometer resulting in no detectable difference from the 0.25 m s^{-1} baseline in the 5-min intervals over which data were averaged. The daily course of transpiration appeared to follow those of both PPFD and VPD. The substantial increase in g_c recorded before PPFD abruptly rose at c. 1200 hours did not result in a corresponding increase in E, presumably because VPD was still relatively low. In gap site 4, PPFD remained below 250 μmol m^{-2} s^{-1} throughout the entire day. Wind speed was low, but in contrast to site 3, frequently above the 0.25 m s^{-1} baseline. Maximum E was substantially lower than in site 3, consistent with lower prevailing PPFD and VPD in site 4.

M. argentea was selected for detailed analysis of stomatal control of transpiration based on its abundance and occurrence in all four study sites. Average g_s of *M. argentea* across all sites was 204 mmol m^{-2} s^{-1} but varied considerably among sites presumably due to variations in PPFD and soil moisture (Table 2). Boundary layer conductance was rather low in relation to g_s causing g_c to be considerably lower than g_s. An additional consequence of the low ratio of g_b to g_s in *M. argentea* was relatively poor stomatal control of transpiration as reflected in values for the decoupling coefficient Ω ranging between 0.70 and 0.79. Thus a 10% change in g_s when g_s was near its mean value would be expected to result in only a

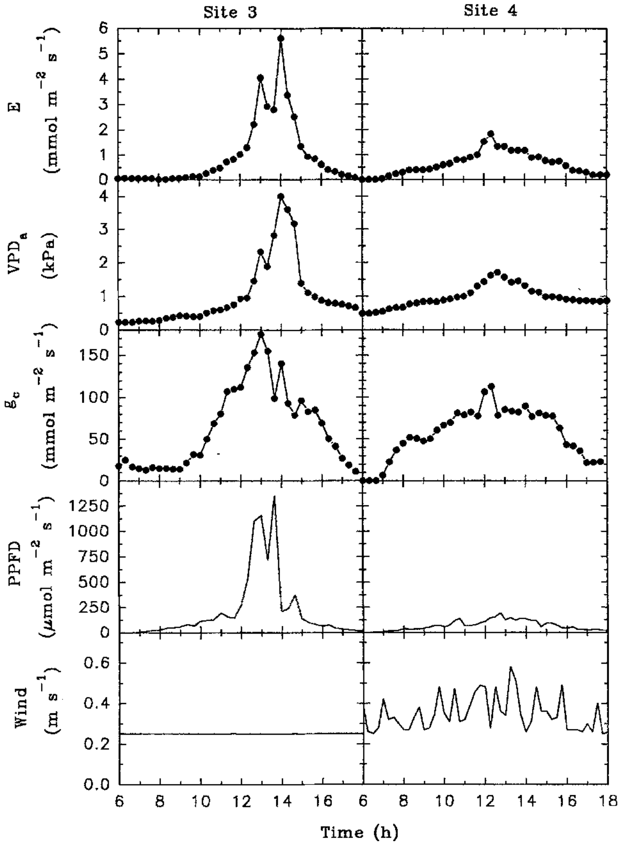

Fig. 1 Representative daily courses of transpiration (*E*) determined with the stem heat balance technique for individual *Miconia argentea* plants in two treefall gap sites during the dry season of 1992. Also shown are leaf-to-air vapor pressure difference (*VPD_a*), total vapor phase conductance (*g_c*), Photosynthetic photon flux density (*PPFD*), and wind speed

Table 2 Vapor phase conductances (g_s, g_c g_b; mmol m^{-2} s^{-1}) and the stomatal decoupling coefficient (Ω) for nine individuals of *Miconia argentea* in four sites on Barro Colorado Island, Panama during the dry seasons of 1991 and 1992. Measurements in Site 4 were obtained from the same group of three individuals during 2 days prior to irrigation (*BI*) and during 2 days following irrigation (*AI*). Values are means (±SE) of *n* determinations. Each of the *n* values of g_s is an average obtained from four leaves

Year	Site	g_s	g_c	g_b	Ω	*n*
1991	1	257 (8)	128 (7)	273 (28)	0.76 (0.01)	13
	2	245 (20)	132 (11)	313 (43)	0.73 (0.02)	12
1992	3	125 (18)	52 (11)	104 (31)	0.75 (0.03)	6
	4 BI	161 (8)	90 (3)	218 (14)	0.70 (0.02)	28
	4 AI	230 (11)	100 (5)	181 (12)	0.79 (0.01)	24
Mean		204	100	218	0.75	

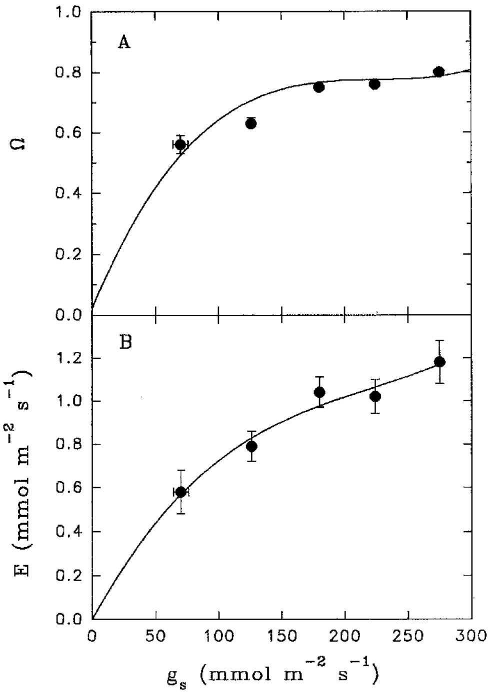

Fig. 2 **A** The stomatal decoupling coefficient (Ω) and **B** transpiration (E) in relation to stomatal conductance (g_s) for *M. argentea* plants growing in three different treefall gaps. *Points* (±SE) are averages of determinations recorded over 50 mmol m^{-2} s^{-1} intervals of stomatal conductance beginning with the interval between 50 and 100 mmol m^{-2} s^{-1}. Some SEs are smaller than the symbols. n=10–20 determinations

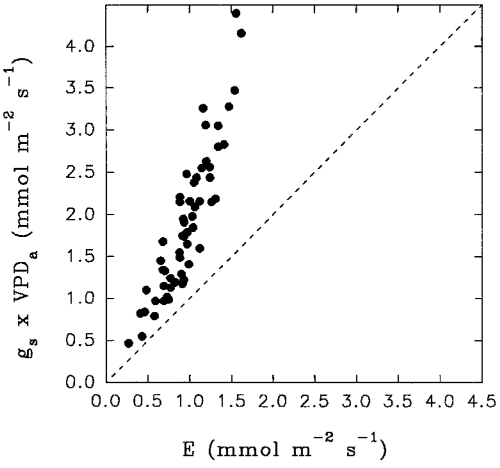

Fig. 3 Predicted transpiration of *M. argentea* in relation to actual transpiration (E) determined from sap flow measurements using the heat balance technique. Predicted transpiration was obtained from the product of stomatal conductance (g_s) and the leaf-to-bulk air vapor pressure difference (VPD$_a$). Each *point* was determined from four to five measurements of g_s and the average sap flow and VPD$_a$ over the interval during which g_s was measured. The *dashed line* represents the 1:1 relationship between predicted and measured transpiration. Data were collected during 4 consecutive days in March 1992 from four individuals growing at Site 4

2.5% change in transpiration. Both g_s and Ω increased markedly following irrigation during the dry season (Table 2). Only 37 mm of rainfall were recorded during the 60 days preceding the irrigation treatment. Average values of Ω were similar for the other species studied, except *P. guianensis* in which Ω was c. 0.6 during the 1992 dry season when g_s was exceptionally low (Table 1).

The strong decoupling influence of the boundary layer in *M. argentea* was apparent in the relationship between Ω and g_s for mean values of g_s calculated over 50 mmol m^{-2} s^{-1} intervals (Fig. 2A). Even at the lowest mean value of g_s recorded (70 mmol m^{-2} s^{-1}), Ω was about 0.6, increasing to 0.8 at g_s=275 mmol m^{-2} s^{-1}, the highest mean value recorded. The diminishing influence on E of progressive increases in g_s was evident in the relationship between concurrent, independent measurements of E and g_s (Fig. 2B). Porometric estimates of transpiration, obtained as the product of g_s and the leaf-to-bulk air VPD without taking g_b into account, were up to 300% higher than actual rates determined from sap flow measurements (Fig. 3). The magnitude of the error associated with porometry-based estimates of transpiration increased sharply with increasing actual transpiration and therefore with increasing g_S (cf. Figs 3 and 2).

Stomatal responses to humidity were examined for *M. argentea*, *C. obtusifolia*, *C. insignis* and *P. guianensis* in two gap sites during the dry seasons of 1991 and 1992. There was no clear response of g_s to variations in VPD calculated using either the bulk air (Fig. 4A) or the leaf surface (Fig. 4B) as reference points for determination of external vapor pressure. However, VPD and PPFD typically covary throughout the day and are known to have offsetting effects on stomatal conductance. In *M. argentea*, for example, g_s initially increased rapidly with PPFD followed by apparent saturation at PPFD<200 µmol m^{-2} s^{-1} (Fig. 5). As seen in Fig. 5, maximum values of g_s at light-saturation differed among individuals growing in the same site. These differences were associated with plant water status and hydraulic properties. These responses were representative of the other gap colonizing species studied. Thus, when VPD was normalized for the influence of variations in PPFD it became clear that g_s decreased curvilinearly with increasing VPD$_a$ (Fig. 4C). Stomata of all four species appeared to respond to increasing evaporative demand in the same manner, especially when the leaf surface was selected as the reference point for determination of external vapor pressure (Fig. 4D). Use of the leaf surface rather than the bulk air as the external reference point for characterizing stomatal responses to humidity yielded a steeper decline in g_s with increasing VPD/PPFD (cf. Fig. 4C and D). In *M. argentea* this stomatal response to humidity appeared to limit the increase in E with increasing evaporative demand (Fig. 6). Transpiration initially increased linearly with VPD$_a$, approaching a maximum value and then appeared to remain relatively constant or even decline slightly with further increases in VPD$_a$. The differences in maximum E shown in Fig. 6 were associated with plant water status and hydraulic properties (data not shown).

Simultaneous, independent measurements revealed that both E (determined from sap flow) and g_s (determined porometrically) were positively correlated with midday Ψ_L across all of the species studied (Fig. 7A,B).

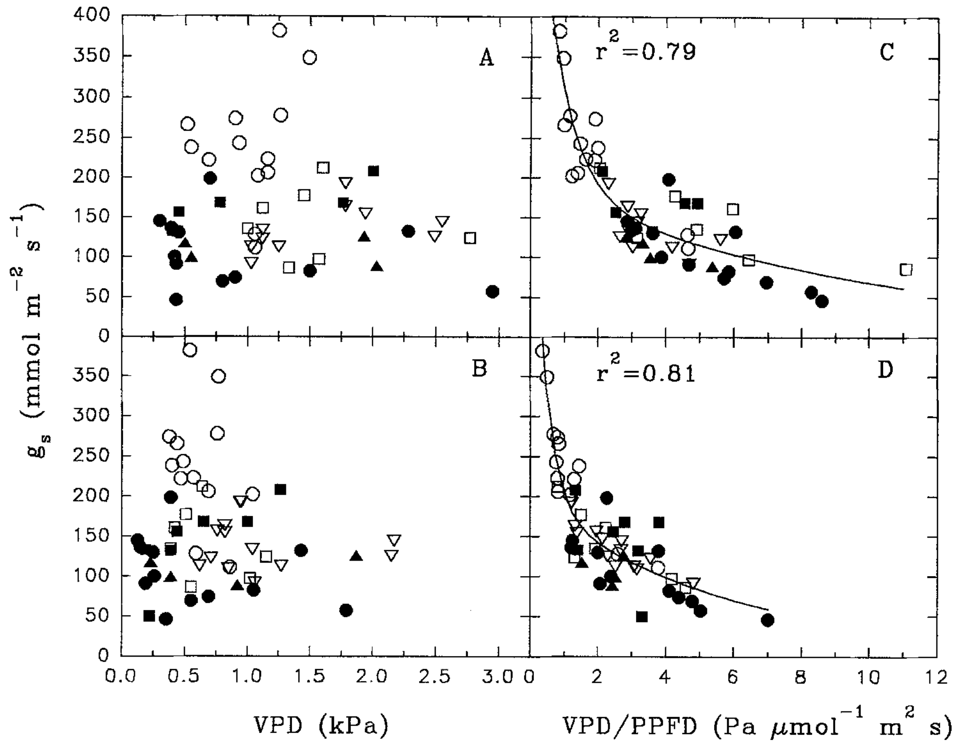

Fig. 4 **A–D** Stomatal conductance (g_s) in relation to leaf-to-air vapor pressure difference (VPD) and VPD normalized by incident photosynthetic photon flux density (VPD/PPFD) for four gap-colonizing species during the 1991 (*open symbols*) and 1992 (*closed symbols*) dry season. Each *point* represents the average of four to five measurements of g_s. In **A** and **C** the bulk air was used as the reference point for determination of external vapor pressure and in **B** and **D** the leaf surface was used as the external reference point. (Symbols: ● ○ *Miconia argentea*, ▼ ▽ *Palicourea guianensis*, ▲ *Cecropia obtusifolia*, ■ □ *C. insignis*)

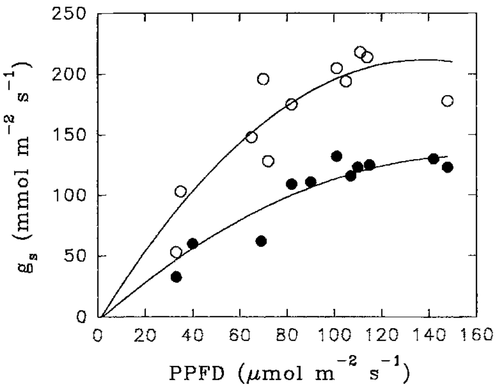

Fig. 5 Stomatal conductance (g_s) in relation to photosynthetically active radiation (PPFD) for two *M. argentea* plants growing in the same treefall gap. Each point represents the average of four to five measurements of g_s. Data were collected during February 1992

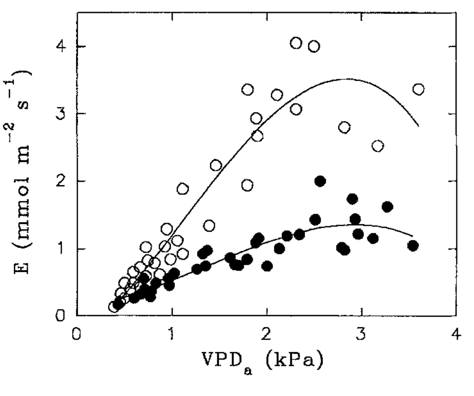

Fig. 6 Transpiration (*E*) in relation to leaf-to-bulk air VPD for two *M. argentea* plants growing in the same treefall gap. Data were obtained from the same individuals as in Fig. 5

However, the relationship between *E* and Ψ_L and between g_s and Ψ_L varied considerably within species. In *P. guianensis*, for example, *E* and g_s remained relatively constant as Ψ_L declined from –1.5 to –2.0 MPa. When *E* and g_s were plotted as functions of the leaf area-specific total hydraulic conductance of the soil/root/leaf pathway (G_t), both *E* and g_s initially increased sharply with increasing G_t, becoming asymptotic at higher values of G_t (Fig. 7C,D). For both *E* and g_s a unique relationship appeared to describe the response of all species to variations in G_t.

Discussion

Our results point to a dominant role for boundary layer properties in determining patterns of transpiration and stomatal behavior in species colonizing treefall gaps in this lowland tropical forest. Boundary layer conductance was roughly equal in magnitude to or often somewhat less than g_s (Table 2) and thus was often the limiting or colimiting conductance to water vapor loss. This would greatly attenuate the impact of moderate variations in g_s on transpiration. Expressed quantitatively as Ω, the decoupling influence of low g_b was predicted to increase from around 0.6 at the lowest values of g_s observed to around 0.8 at the highest values of g_s observed (Fig. 2). The increase in g_s and Ω in *M. argentea* following irrigation during the dry season suggests that stomatal control of transpiration of this and probably other species occurring in treefall gaps would be even weaker during the wet season.

Independent measurements of transpiration and g_s confirmed that progressive increases in g_s had a steadily

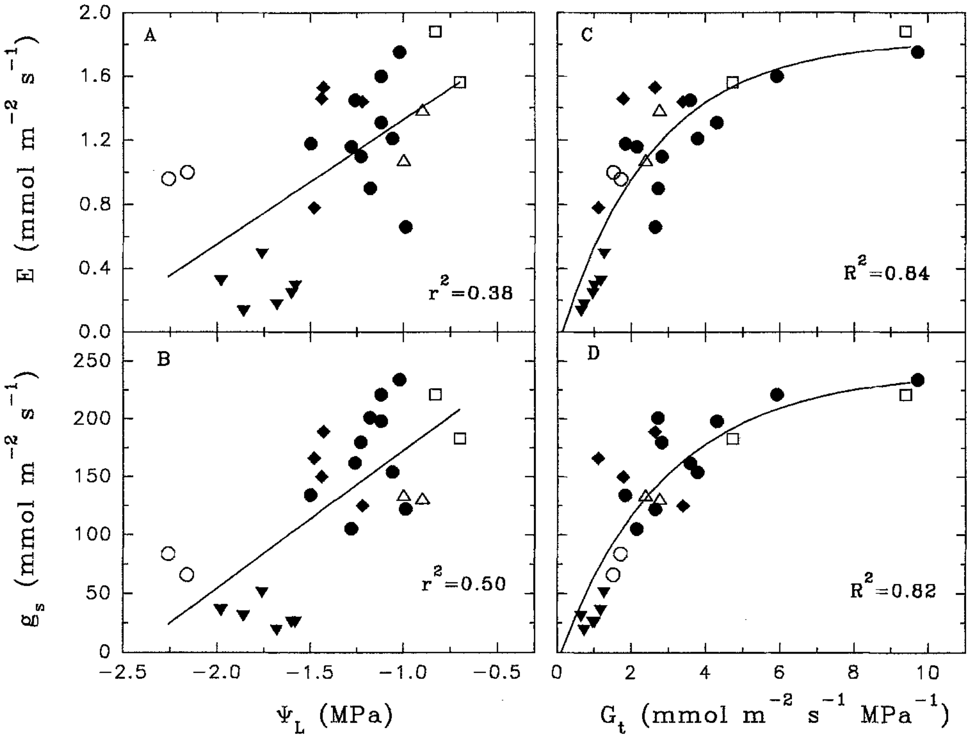

Fig. 7 **A,C** Transpiration (E) and stomatal conductance (**B,D**) (g_s) in relation to midday leaf water potential (Ψ_L) and leaf area-specific total hydraulic conductance of the soil/root/leaf pathway (G_t) for five gap-colonizing species during the dry season of 1992. Each measurement of E represents a 20-min average and g_s the average of four to five determinations per individual. (● ○ *M. argentea* in two sites, ▼ *P. guianensis*, △ *C. obtusifolia*, □ *C. insignis*, ◆ *Coccoloba manzanillensis*)

diminishing influence on E (Fig. 2). Nevertheless, the increase in E with increasing g_s shown in Fig. 2 was greater than would be predicted from the magnitude of Ω (Fig. 2). This was probably attributable to the simultaneous variation of g_s, PPFD and VPD. The average value of Ω determined for treefall gap colonizing species in the present study was consistent with the value of 0.78 estimated by Roberts et al. (1990) for understory species in an Amazonian terra firme rain forest. In the case of *M. argentea* and *Cecropia* spp. which attain heights of 10–20 m, g_b would be expected to increase and Ω decrease as the foliage reaches the more exposed portions of the forest canopy. Nevertheless, if leaves are large and closely spaced, Ω may remain high even in the upper canopy. In *Anacardium excelsum*, for example, which occurs in the forest surrounding our study sites, Ω was about 0.5 in a relatively exposed 35-m-tall individual during the dry season (Meinzer et al. 1993).

Leaf size and wind speed are considered to be the major determinants of g_b. Although leaf movement associated with gusts of wind was sometimes visible, particularly at over 2 m above the forest floor, wind speed near the leaves of the species studied was often below the 0.25 m s^{-1} detection threshold of the anemometer used. The average value of g_b for *M. argentea* was approximately 218 mmol m^{-2} s^{-1}, ranging from 104 to 313 mmol m^{-2} s^{-1} among sites. Values of g_b were similar among the other species studied despite variations in leaf size and shape. Roberts et al. (1990) estimated a g_b value of 240 mmol m^{-2} s^{-1} for understory vegetation in an Amazonian forest using an independent method. The uniformity of g_b among species in these tropical forest gap and understory environments suggests that wind speed played a more important role than leaf size and shape in determining g_b. The ability of conventional models relying on leaf dimensions and wind speed to predict g_b in these sites will be constrained by the difficulty of measuring the extremely low windspeeds. Furthermore, conventional measurements of windspeed at a reference point several m away from the leaves of the plants under study are undoubtedly inadequate in characterizing the attenuation of wind by neighboring plants and leaves as the leaf surface is approached.

These relationships have far-reaching consequences for interpretation of measurements obtained with conventional ecophysiological techniques such as porometry (e.g., Fig. 3) and single-leaf photosynthetic gas exchange measurements in cuvettes. When g_b is low in relation to g_s, measurements of g_s alone do not provide enough information to evaluate the physiological consequences of contrasting patterns of stomatal behavior in different species. With other variables held constant, plant water status is governed largely by the actual flux of water vapor rather than g_s. Thus, when Ω is large, relatively large differences in g_s do not necessarily imply equivalent differences in water use and plant water balance (Fig. 3). Similarly, observations of dynamic responses of gas exchange in tropical forest gap and understory species to light flecks in well ventilated cuvettes may not be representative of the behavior of leaves unenclosed by cuvettes. In a ventilated cuvette g_b is typically high, allowing stomatal movements to have a large impact on transpiration (low value of Ω). In an unenclosed leaf, the net response of transpiration to a light fleck will depend on the change in leaf temperature and the degree of humidification of the boundary layer resulting from increased g_s.

The lower g_b of unenclosed leaves will increase the total resistance to diffusion of CO_2 into the leaf resulting in a steeper gradient between the ambient and intercellular CO_2 partial pressure than in an illuminated leaf enclosed in a ventilated cuvette.

An additional consequence of the low values of g_b observed was to partially obscure stomatal responses to humidity by uncoupling the vapor pressure at the leaf surface from that in the bulk air. It is particularly noteworthy that stomata of all five species studied appeared to respond to increasing evaporative demand in a similar manner, especially when the leaf surface was selected as the reference point for determination of external vapor pressure and when the simultaneous variation of stomatal opening and closing stimuli (i.e., PPFD and VPD) was taken into account (Fig. 4). These results and those of Bunce (1985) raise the possibility that contrasting stomatal responses to similar leaf-to-bulk air VPD may be governed as much by the external boundary layer as by intrinsic physiological differences among species. There are indications in the literature that maximum g_s is higher in species with large leaves (Körner et al. 1979; Grace et al. 1982). It is not known whether this pattern reflects a stomatal response to humidification of air at the leaf surface mediated by low g_b or whether it is an intrinsic physiological correlate of large leaf size. Further research on patterns of g_s in relation to g_b under well defined conditions in the field is needed to evaluate the relative roles of microenvironment, leaf size and phylogeny in determining maximum levels of g_s. If low boundary layer conductance is expected, as in plants with large leaves, in dense canopies, or in sites with low windspeed, it is desirable to use the leaf surface as the external reference point for characterizing stomatal responses to atmospheric variables such as humidity and CO_2. This would require measurement of fluxes and conductances at at least two scales of observation: porometric measurements of g_s in single leaves and concurrent measurements of the actual water vapor flux from unenclosed branches or entire plants. Despite the decoupling influence of the boundary layer, it was clear that the strong stomatal response to humidity in *M. argentea* limited the increase in E with increasing evaporative demand (Fig. 6).

Scaling between single leaf porometric measurements and whole plant measurements of sap flow in the present work was facilitated by the relatively small size of the individuals selected for study. Larger shrubs and trees would present potential sampling problems arising from the effects of differences in leaf age and differences in exposure to light and wind on stomatal conductance.

The surprising pattern shown in Fig. 7 suggests that stomata of all five species responded to changes in water transport efficiency on a leaf area basis in the same manner and that stomatal adjustments to changing G_t coordinated transpiration with water transport efficiency rather than bulk leaf water status. The initial sharp increase in E with increasing G_t followed by a greatly diminished response of E to further increases in G_t (Fig. 7C) appeared to be consistent with a steadily diminishing impact of increasing g_s on E (Fig. 2). This response would be expected from increasing g_s/g_b and therefore increasing Ω (Fig. 2). However, independent measurements revealed that g_s also did not increase continuously with G_t (Fig. 7D). Thus, some other unidentified factor limited the rate of increase in g_s with increasing G_t thereby limiting E at higher levels of G_t.

The relationship between g_s and G_t obtained in the present study was similar to the relationship between g_s and leaf area-specific root hydraulic conductance reported for sugarcane by Saliendra and Meinzer (1989). More recently, comparable relationships between E, g_s and G_t were reported by Sperry and Pockman (1993) for *Betula occidentalis* plants in which variation in G_t was obtained by inducing cavitation in the xylem. The mechanism linking g_s and therefore transpiration to variation in G_t is not known. Meinzer et al. (1991) have proposed that chemical signals transported from the roots to the leaves in the transpiration stream are responsible for the developmental coordination of stomatal and root hydraulic conductance in well-irrigated sugarcane. However, it seems unlikely that root signals were involved in stomatal responses to manipulation of stem hydraulic properties observed by Sperry and Pockman (1993).

Our results suggest that differences in stomatal behavior and transpiration in the field may not necessarily reflect intrinsic differences in plant responsiveness to environmental variables such as evaporative demand. Selection of the leaf surface as the reference point for characterizing external humidity and of G_t as a measure of the availability and efficiency of delivery of water per unit leaf area served, yielded similar patterns of stomatal behavior among several phylogenetically diverse species. Even though intrinsic responsiveness to a given variable may not differ among species, morphological and external factors such as rooting patterns and soil water distribution may lead to different physiological operating ranges thereby enhancing partitioning of water resources and diminishing competitive interactions. Consistent with this, concurrent measurements of soil and xylem water hydrogen isotope (δD) values and leaf water potential during the dry season in sites where the present study was carried out led Jackson et al. (1995) to conclude that a high degree of soil water partitioning exists among both gap colonizing and shade tolerant species. Roots of *M. argentea* were able to utilize deeper, more abundant soil water at a depth of at least 1 m, while water uptake by roots of *P. guianensis* was apparenly restricted to the portion of the soil profile above 0.4 m depth (Jackson et al. 1995).

Synergistic interactions between physiological and environmental variables must also be considered in interpreting patterns of stomatal behavior. For example, among plants with similar g_b, lower G_t in some would result in reduced stomatal opening potential and therefore reduced humidification of the boundary layer leading to higher values of VPD at the leaf surface which would further reduce stomatal opening potential. The mechanisms by which stomata balance transpiration with evaporative demand and water transport efficiency remain to be elucidated.

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