

Stomatal and environmental control of transpiration in a lowland tropical forest tree

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ABSTRACT

Stomatal control of crown transpiration was studied in *Anacardium excelsum*, a large-leaved, emergent canopy species common in the moist forests of Central and northern South America. A construction crane equipped with a gondola was used to gain access to the uppermost level in the crown of a 35-m-tall individual. Stomatal conductance at the single leaf scale, and transpiration and total vapour phase conductance (stomatal and boundary layer) at the branch scale were measured simultaneously using the independent techniques of porometry and stem heat balance, respectively. This permitted the sensitivity of transpiration to a marginal change in stomatal conductance to be evaluated using a dimensionless coupling coefficient ($1-\Omega$) ranging from zero to 1, with 1 representing maximal stomatal control of transpiration. Average stomatal conductance varied from $0.09 \text{ mol m}^{-2} \text{ s}^{-1}$ during the dry season to $0.3 \text{ mol m}^{-2} \text{ s}^{-1}$ during the wet season. Since boundary layer conductance was relatively low ($0.4 \text{ mol m}^{-2} \text{ s}^{-1}$), $1-\Omega$ ranged from 0.46 during the dry season to only 0.25 during the wet season. A pronounced stomatal response to humidity was observed, which strongly limited transpiration as evaporative demand increased. The stomatal response to humidity was apparent only when the leaf surface was used as the reference point for measurement of external vapour pressure. Average transpiration was predicted to be nearly the same during the dry and wet seasons despite a 1 kPa difference in the prevailing leaf-to-air vapour pressure difference. The patterns of stomatal behaviour and transpiration observed were consistent with recent proposals that stomatal responses to humidity are based on sensing the transpiration rate itself.

Key-words: *Anacardium excelsum*; stomata; transpiration; humidity; tropical forest.

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Abbreviations: E , transpiration per unit leaf area; g , conductance per unit leaf area (g_{bl} , boundary layer, g_c , crown, g_s , stomatal); V , leaf-air vapour pressure difference (V_s , at leaf surface, V_a , in bulk air ca. 1 m away from leaves); $1-\Omega$, leaf-atmosphere coupling coefficient.

INTRODUCTION

The extent to which stomatal movements control canopy transpiration is determined largely by 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. This prevents transpiration from promoting local equilibration of humidity near the leaf within the boundary layer that would uncouple the vapour pressure and evaporative demand at the leaf surface from that in the bulk air. The degree to which the ambient vapour pressure is imposed at the leaf surface has been described quantitatively in terms of a dimensionless coupling coefficient ($1-\Omega$) ranging from zero to 1, with 1 representing maximal stomatal control of transpiration (McNaughton & Jarvis 1983; Jarvis & McNaughton 1986). For example, in aerodynamically rough coniferous trees with their relatively low stomatal conductance and high boundary layer conductance, the vapour pressure in the bulk air is imposed nearly at the leaf surface resulting in strong stomatal control of transpiration ($1-\Omega \approx 0.9$).

In contrast to many temperate forests, tropical forests contain a wide variety of emergent canopy species and associated variation in stomatal conductance, canopy structure and roughness. Although detailed knowledge of patterns of $1-\Omega$ in species-diverse tropical forests is essential for predicting the effects of species composition on evapotranspiration and regional water balance, few data are available. Recently, considerable information on patterns of variation in stomatal conductance of tropical trees has begun to accumulate (e.g. Whitehead, Okali & Fasehun 1981; Grace, Okali & Fasehun 1982; Roberts, Cabral & De Aguiar 1990; Dolman et al. 1991). Nevertheless, reports of *in situ* measurements of stomatal conductance in the upper canopy of tropical forests are still rare. Even

fewer attempts have been made to partition leaf, crown and canopy conductance between their stomatal and boundary layer components, thereby obtaining an estimate of $1-\Omega$ (Roberts et al. 1990).

Anacardium. excelsum (Bertero & Balb.) Skeels is a large-leaved, emergent canopy species common in the moist forests of Central and northern South America. Although annual rainfall is high (2000–3000 mm) in these forests, it exhibits a pronounced seasonal distribution in which several consecutive months are nearly rainless. Associated with this rainfall regime is a variety of leaf phenologies among tree species ranging from evergreen to briefly deciduous to entirely deciduous during the dry season (Wright & Cornejo 1990). Stomatal responses to environmental variables such as air saturation deficit might be expected to covary with leaf phenology, but there seems to be little published information available on this topic. The essentially evergreen habit of *A. excelsum* makes it a suitable species in which to study the influence of seasonal variation in environmental variables on stomatal response and stomatal control of transpiration. In the present study, independent measurements of stomatal conductance of individual leaves and transpiration from intact branches were made simultaneously in the upper and lower crown of a 35-m-tall *A. excelsum* tree. Our objectives were to integrate measurements at the single-leaf and crown levels in order to: (1) estimate the degree to which stomatal movements control transpiration; (2) determine the extent to which stomata responded to evaporative demand; and (3) probe the extent to which transpiration was controlled by this response.

MATERIALS AND METHODS

Field site and plant material

A construction crane equipped with a gondola was used to gain access to the uppermost level in the crown of a 35 m-tall *A. excelsum* tree growing in a 2 ha remnant of natural forest near Panama City, Panama (lat 9° 10' N, long 79° 51' W, alt. ca. 50 m). The gondola (ca. 1.5 × 1.5 × 2.5 m) was attached with cables to a rotating boom, and could be manoeuvred both horizontally and vertically with precision. The relatively open forest remnant contained evergreen or briefly deciduous species such as *Luehea seemannii*, *Ficus obtusifolia* and *Cecropia* spp., and dry season deciduous species such as *Pseudobombax septenatum*. *Anacardium excelsum* is often briefly deciduous early in the dry season and was one of the dominant species on the site. The crown of the individual selected for study spanned a vertical distance of approximately 25 m. The leaves were about 25 cm long and 12 cm wide, and were supported by a short, rigid petiole that noticeably restricted their movement. The mean annual rainfall at the site is about 2000 mm, of which less than 200 mm falls during the dry season between January and April. Measurements were made during February and March 1991, and again during September in the middle of the wet season.

Transpiration

Transpiration (E) was measured as mass flow through individual intact branches using a heat balance method as described by Baker & Van Bavel (1987). This method has been applied successfully to woody species growing under field conditions (e.g. Steinberg, van Bavel & McFarland 1989; Heilman & Ham 1990; Steinberg, McFarland & Worthington 1990). Sap flow gauges (Dynamax Inc., Houston, TX, USA), consisting of a heating element, a thermopile and individual thermocouples were attached to terminal branches several nodes away from the branch apex. Total leaf area distal to the gauges was typically 0.4–1.5 m². 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, UT, USA) equipped with a 32-channel multiplexer (AM 416, Campbell Scientific) permitted several gauges to be operated simultaneously. Data were recorded continuously and stored in a solid state storage module (SM 196, Campbell Scientific). Measurements were made in the upper crown at a height of about 30 m on 4 consecutive days during February and in the lower crown at a height of about 15 m on 4 consecutive days during March. After securing the data acquisition components and batteries to a major branch, sap flow gauges were installed on five exposed terminal branches. The gauges and adjacent portions of 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. 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 h local time when transpiration was assumed to be zero. The same procedures were used to measure sap flow during February and March in five individuals of the woody species *Miconia argentea* (Sw.) DC. and two individuals of *Cecropia obtusifolia* Bertol. growing in nearby gaps in the forest. When the plants were subsequently decapitated and the bases of their stems installed in potometers, simultaneous sap flow gauge and transpiration measurements were within 10% of each other (F. C. Meinzer et al., unpublished observations). Upon completion of the measurements, leaves were removed from the branches for determination of their area in an area meter (model 3100, LI-COR, Inc., Lincoln, NE, USA). All values of E reported here are on a unit plan leaf area basis. Sap flow was not measured during the wet season.

Stomatal conductance

During the dry season stomatal conductance (g_s) was measured with a steady state porometer (model 1600, LI-COR Inc.) in four to five leaves on each of the five branches fit-

ted with sap flow gauges. Typically, three to four complete sets of measurements were obtained between 0800 and 1600 h on the 4 consecutive days during which sap flow was determined in the upper and lower crown. During the wet season g_s was measured only in the upper crown. The ratio of abaxial to adaxial conductance for these hypostomatous leaves was about 21. All values of g_s reported are of the abaxial leaf surface.

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. Ambient vapour pressure was measured by pumping air obtained at a distance of approximately 1 m from the foliage through a chilled mirror dew point hygrometer (model Dew-10, General Eastern, Watertown, MA, USA, inside a Campbell Scientific, Corp. model O23 Bowen ratio system enclosure). Ambient temperature 1 m away from the foliage, and leaf temperature were determined with fine wire (0.08 mm) copper-constantan thermocouples. For leaf temperature one thermojunction was affixed to the abaxial surface of each of four leaves on each of the five branches 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 vapour pressure difference between the leaf interior and the bulk air (V_a) was calculated using saturation vapour pressure at leaf temperature and the ambient vapour pressure. Crown conductance (g_c ; mol m⁻² s⁻¹) was calculated as

$$g_c = \frac{E}{V_a/P} \quad (1)$$

where P is atmospheric pressure. All values of g_c are expressed on a unit plan leaf area basis. Crown conductance as defined here includes a stomatal component, and boundary layer components determined both by leaf dimensions and by attenuation of wind by the surrounding forest canopy. Therefore, it can be regarded as partially

analogous to a canopy conductance, even though the latter is traditionally expressed on a unit ground area basis. Boundary layer conductance (g_{bl}) was calculated from g_c and g_s as

$$g_{bl} = 1/(1/g_c - 1/g_s) \quad (2)$$

Stomatal control of transpiration

The sensitivity of transpiration to a marginal change in g_s was evaluated using $1-\Omega$ after the procedure of Jarvis & McNaughton (1986) with a modification proposed by Martin (1989) that takes the radiative coupling between leaves and the atmosphere into account. This dimensionless coupling coefficient was defined as

$$1-\Omega = 1 - \frac{\epsilon + 2 + g_r/g_{bl}}{\epsilon + 2 + (g_{bl} + g_r)/g_s + g_r/g_{bl}} \quad (3)$$

where ϵ is the ratio of the increase of latent heat content to increase of sensible heat content of saturated air and $g_r = 4\epsilon\sigma T_a^3/\rho C_p$ is a long-wave radiative transfer 'conductance' of the canopy where ϵ is emissivity (0.97), σ is the Stefan-Boltzmann constant, T_a is air temperature (K), ρ is the density of air, and C_p is the specific heat of air at constant pressure. This definition of $1-\Omega$ follows that of McNaughton & Jarvis (1991) for a hypostomatous leaf symmetrical with respect to boundary layer conductance. Estimates of $1-\Omega$ during the wet season were obtained from measurements of g_s in the upper crown and the average g_{bl} determined during the dry season. The leaf surface was used as an additional external reference point for characterizing stomatal response to evaporative demand and its consequences for transpiration. The leaf-to-air vapour pressure difference at the leaf surface (V_s ; kPa) was estimated as

$$V_s = EP/g_s \quad (4)$$

RESULTS

On clear days during the dry season, the diurnal course of E was similar in both the upper and lower crown (Fig. 1). In the upper crown, E typically attained a maximum value at mid-morning, after which it declined relatively sharply until mid-afternoon when a transient increase was usually observed. In the lower crown, E increased more slowly during the morning attaining its maximum value approximately 2 h later than in the upper crown. The diurnal course of g_c generally paralleled that of E .

There were no significant differences in average g_s , g_c , g_{bl} and V_a in the upper and lower crown (Table 1). The transpiration rate and the level of stomatal control of transpiration ($1-\Omega$) were nearly identical in the upper and lower crown, consistent with the uniformity of conductances and the driving force for water loss at the two

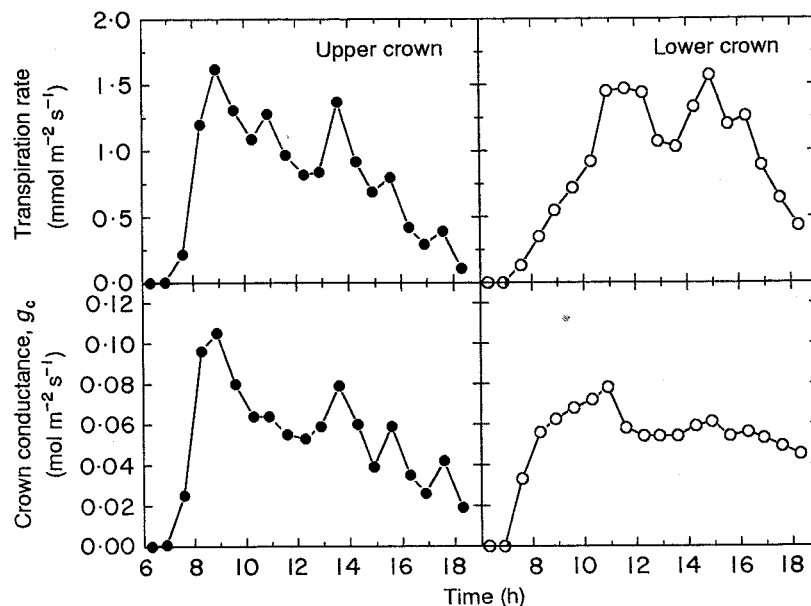


Figure 1. Diurnal courses of transpiration and crown conductance on a unit leaf area basis in the upper and lower crown of an *Anacardium excelsum* tree on two different days during the dry season. Points are means of five branches.

heights. Leaf temperatures were slightly higher in the lower ($30.2 \pm 0.4^\circ\text{C}$) than in the upper ($29.7 \pm 0.3^\circ\text{C}$) crown, but were typically within 2°C of air temperature.

During the wet season, g_s was $0.3 \pm 0.04 \text{ mol m}^{-2} \text{ s}^{-1}$ in the upper crown. Leaf and air temperatures were similar to those measured during the dry season and ranged from 28.8 to 30.6°C during the periods when g_s was being measured. Since ambient humidity was higher during the wet season, V_a was only about 0.8 kPa , considerably lower than the average V_a of 1.8 kPa measured during the dry season.

The relationship between $1-\Omega$ and g_s was determined over the range of g_s measured during the dry and wet seasons using the average value of g_{bl} determined during the dry season (Fig. 2a). Because of higher g_s during the wet

season, $1-\Omega$ was predicted to vary between 0.2 and 0.4 compared with 0.4 and 0.7 during the dry season when the ratio of g_s to g_{bl} was much lower. There was little seasonal overlap because the lowest values of g_s observed during the wet season coincided with the maximum values of g_s observed during the dry season. The operating range of E was predicted to be similar during the dry and wet seasons despite the large seasonal difference in the operating range for g_s (Fig. 2b). The seasonal stability of E was attributable to both the lower evaporative demand during the wet season and the reduced sensitivity of E to changes in g_s .

There was no clear response of g_s to variations in V_a determined as the difference between saturation vapour pressure at leaf temperature and the vapour pressure of the bulk air (Fig. 3a). However, when the leaf surface was used as a reference point to calculate V_s (equation 4), g_s was observed to decline sharply with increasing evaporative demand (Fig. 3b). For measurements obtained between about 8 h and 15 h local time, a single function described the relationship between g_s and V_s for both the upper and lower crown regardless of variations in irradiance. Independent, nonporometric estimates of the total vapour phase conductance of the crown (g_c) from the sap flow measurements showed that g_c declined with increasing V_a (Fig. 4). This was consistent with the response of g_s to V_s (Fig. 3b).

When E was plotted as a function of V_s , it was found that after increasing initially with V_s , E approached a maximum value and remained nearly independent of V_s over most of the range of V_s observed during the dry season (Fig. 5a). This strong limitation of E with increasing V_s resulted from progressive stomatal closure with increasing V_s (Fig. 3b). If g_s had been maintained at its maximum

Table 1. Vapour phase conductances, leaf-to-bulk air vapour pressure difference, transpiration and stomatal control of transpiration in the upper and lower crown of an *Anacardium excelsum* tree during the dry season*

	Conductance ($\text{mol m}^{-2} \text{ s}^{-1}$)			V_a (kPa)	E ($\text{mmol m}^{-2} \text{ s}^{-1}$)	$1-\Omega$
	g_s	g_c	g_{bl}			
Upper canopy	0.090 (0.005)	0.058 (0.003)	0.421 (0.114)	1.84 (0.08)	1.05 (0.06)	0.46 (0.04)
Lower canopy	0.092 (0.006)	0.060 (0.004)	0.346 (0.062)	1.81 (0.11)	1.02 (0.03)	0.46 (0.04)

*Standard errors are shown in parentheses ($n=26$, upper crown; $n=27$, lower crown). Average values of g_s for 4–5 leaves on a given branch fitted with a sap flow gauge were treated as individual values to obtain the overall averages shown.

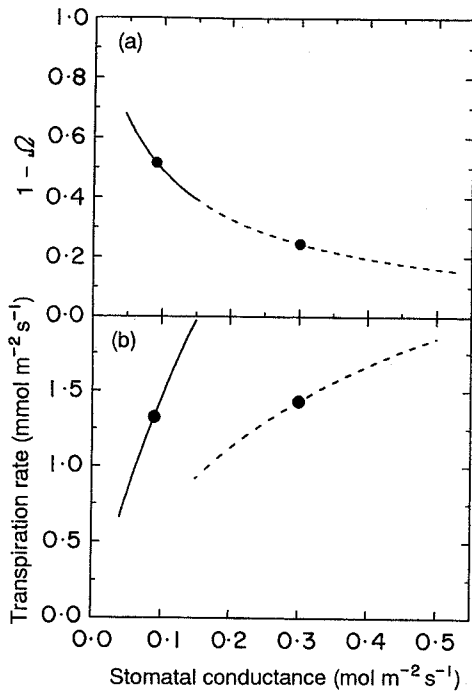


Figure 2. (a) The stomatal coupling coefficient over the range of stomatal conductance observed during the dry (solid line) and wet (dashed line) seasons. The symbols represent the average values for each season. (b) Transpiration in relation to stomatal conductance during the dry (solid line) and wet (dashed line) seasons. V_a was held constant at 1.8 and 0.8 kPa during the dry and wet seasons, respectively. See text for further details.

value despite increasing evaporative demand, then E would have increased linearly with V_s (Fig. 5A, dashed line) and would have been about twice as high as the actual E at $V_s = 1.5$ kPa. The positive relationship between $1 - \Omega$ and V_s (Fig. 5b) was consistent with progressively tighter stomatal control of E as evaporative demand increased (cf. Figs. 3b & 5a). The stomatal coupling coefficient increased fourfold from 0.2 at the minimum value of V_s to 0.8 at the maximum value of V_s observed during the dry season. Both passive and active, stomatally-mediated components probably contributed to these variations in $1 - \Omega$. For example, passive variation in $1 - \Omega$ could arise from fluctuations in wind speed which would alter both g_{bl} and V_s . The resulting variation in g_s/g_{bl} would cause $1 - \Omega$ to vary independently of stomatal adjustment to changing V_s . Active variation in $1 - \Omega$ would result from stomatal adjustment to fluctuations in V_s associated with variations in either leaf temperature or wind speed.

Crown transpiration predicted from porometric measurements of g_s (as $g_s \times V_a$) was generally 10–100% higher than actual E determined from simultaneous measurements of sap flow (Fig. 6). Considerable variation among measurements in the decoupling influence of the boundary layer thus prevented an empirical correction factor from being derived for prediction of E from conventional measurements of g_s and V_a .

DISCUSSION

To our knowledge, the data presented here represent some of the first direct measurements of E and its diurnal variation in the upper crown of an individual tropical tree species. Most studies of transpiration in tropical forests have relied on either micrometeorological techniques to estimate total evapotranspiration from extensive areas of mixed forest canopy (e.g. Doley 1981; Shuttleworth 1988) or on porometric measurements of g_s and indirect estimates of g_{bl} to predict transpiration of individual species (e.g. Grace *et al.* 1982; Roberts *et al.* 1990). The results obtained with *A. excelsum* illustrate the importance of taking the decoupling influence of the leaf and canopy boundary layers into account when attempting to predict E from single leaf measurements of g_s (Fig. 6). The scatter among the data shown in Fig. 6 suggests that predictions of instantaneous E from g_s and V_a could deviate widely from actual values even if g_s were used with an estimate of average g_{bl} to compute the total vapour phase conductance that actually limits water loss. Nevertheless, Dolman *et al.* (1991) reported reasonably good agreement between canopy transpiration measured with the eddy correlation technique and transpiration estimated by incorporating porometric measurements into a multi-level model for an Amazonian forest.

Leaf boundary layer conductance of *A. excelsum* was determined from simultaneous measurements of vapour fluxes, driving forces, and conductances at both the single

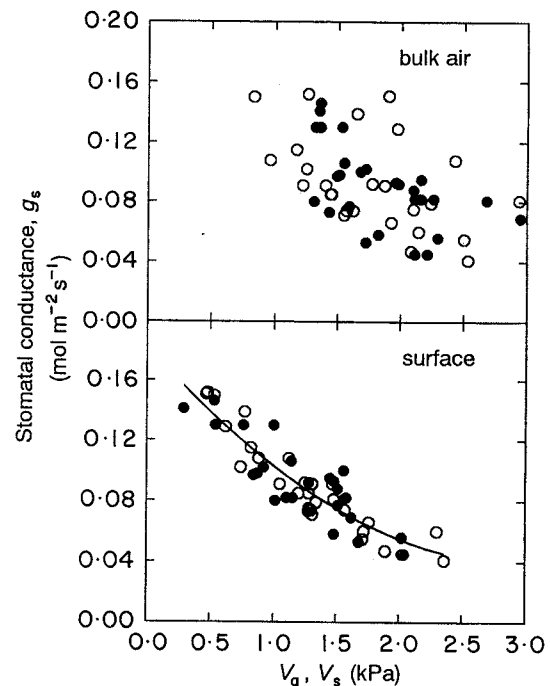


Figure 3. Stomatal conductance in relation to the leaf-to-air vapour pressure difference in the upper (●) and lower (○) crown during the dry season. Vapour pressure difference was determined using an external reference point in the bulk air ca. 1 m away from the leaves (V_a) and at the leaf surface (V_s).

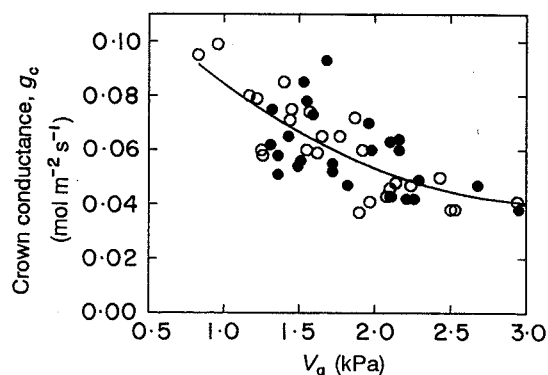


Figure 4. Crown conductance on in relation to V_a during the dry season. Symbols as in Fig. 3.

leaf and crown scales. Values of g_{bl} obtained by using g_s and g_c in Eqn 2 are potentially subject to large uncertainty. Nevertheless, the values of g_{bl} obtained using Eqn 2 were similar to those determined from brass models of the large-leaved tropical trees *Tectona grandis* and *Gmelina arborea* at a wind speed of 2 m s^{-1} (Grace, Fasehun & Dixon 1980). Wind speed was not measured in the present study, but values reported by Windsor (1990) for the upper canopy of forest on nearby Barro Colorado Island (BCI) suggest that $1.5\text{--}2 \text{ m s}^{-1}$ is a realistic range for the dry season. During the wet season, however, average wind speed for the upper canopy on BCI is only about 0.7 m s^{-1} . Assuming that g_{bl} in *A. excelsum* increases linearly with wind speed between 0 and 2 m s^{-1} in a manner similar to that reported for *T. grandis* and *G. arborea*, then average g_{bl} during the wet season may have been about $0.25 \text{ mol m}^{-2} \text{ s}^{-1}$. Under these conditions, average $1-\Omega$ for *A. excelsum* during the wet season would be less than 0.2 rather than the value of 0.25 calculated using g_{bl} values obtained during the dry season.

In contrast to the similar magnitude of g_{bl} among *T. grandis*, *G. arborea* and *A. excelsum*, g_s of *T. grandis* and *G. arborea* (Whitehead *et al.* 1981; Grace *et al.* 1982) was more than twice as high as that measured for *A. excelsum*. The corresponding higher ratios of stomatal to boundary layer conductance in *T. grandis* and *G. arborea* would be expected to result in weaker stomatal control of E in these species than in *A. excelsum*. Using measurements of g_s and g_{bl} reported for *T. grandis* and *G. arborea*, Jarvis and McNaughton (1986) estimated that $1-\Omega$ would range from 0.1 to 0.2, even lower than the average values of 0.25 to 0.46 estimated for *A. excelsum* in the present study. These values of $1-\Omega$ estimated for *T. grandis*, *G. arborea* and *A. excelsum* are considerably lower than the average value of about 0.7 calculated for upper canopy species in an Amazonian forest (Roberts *et al.* 1990). The source of this variation in levels of stomatal control of E among study sites seems to be larger values of g_{bl} estimated for the upper canopy of the Amazonian forest rather than lower values of g_s . Thus, in contrast to temperate coniferous forests which are considered to have uniformly high values of $1-\Omega$ of about 0.9 (Jarvis & McNaughton, 1986), tropical forests

may be characterized by lower overall values of $1-\Omega$ and considerable variation in the extent of stomatal control of transpiration among upper canopy species.

Stomatal conductance in *A. excelsum* declined sharply in response to increasing evaporative demand imposed at the leaf surface (Fig. 3b). Despite considerable physiological data demonstrating a stomatal response to humidity in numerous species (Grantz 1990), it has been suggested that these responses may be no more than an artifact associated with enclosure of leaves in porometers or cuvettes (Idso 1987; Idso, Allen & Choudhury 1988). The negative correlation between g_c of unenclosed branches and V_a (Fig. 4) strongly suggests that the apparent response of g_s to V_s (Fig. 3b) was not an artifact associated with porometric measurements. However, the results shown in Figs 3 and 4 point to the importance of considering the influence that scale and choice of reference points for measurements of environmental variables have on interpretation of experimental results (Jarvis & McNaughton 1985; Grantz & Meinzer 1990). In the present study, for example, the stomatal response to evaporative demand would not have been apparent from conventional measurements of V_a and porometric measurements of g_s (Fig. 3a). The unique relationship between g_s and V_s in the upper and lower crown (Fig. 3b) regardless of variations in irradiance (data not shown) is consistent with observations by Roberts *et al.* (1990) showing g_s in several Amazonian rain forest upper canopy species to be nearly independent of solar radiation above about 400 W m^{-2} .

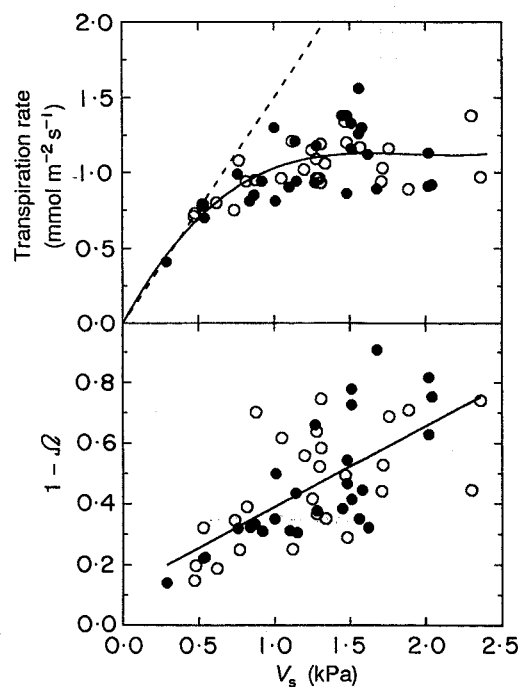


Figure 5. (a) Transpiration in relation to V_s during the dry season. The dashed line represents the relationship between transpiration and V_s with stomatal conductance held constant at its maximum value observed during the dry season. Symbols as in Fig. 3. (b) The stomatal coupling coefficient in relation to V_s during the dry season.

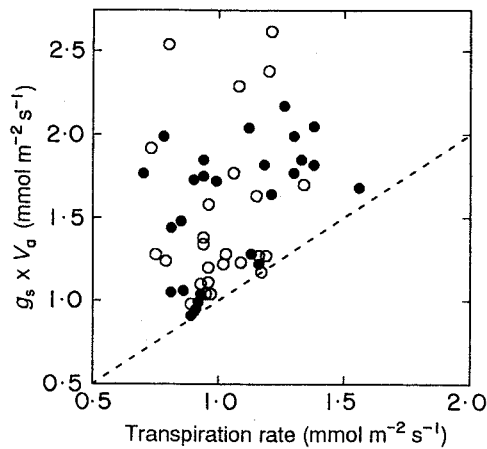


Figure 6. Transpiration predicted as $g_s \times V_a$ in relation to actual transpiration determined independently from sap flow measurements. The dashed line represents a 1:1 relationship between predicted and measured transpiration. Symbols as in Fig. 3.

Higher g_s during the wet season was consistent with higher ambient humidity and reduced evaporative demand. Nevertheless, average values of g_s during the wet season were considerably higher than the maximum values observed during the dry season at low V_s (Figs. 2 & 3) suggesting that seasonal adjustments in g_s were not attributable entirely to the seasonal variation in evaporative demand. Previous measurements of g_s in *Anacardium excelsum* and other tropical tree species suggest that leaf age may have been an additional factor contributing to the seasonal variation in g_s observed in the present study. *A. excelsum* often exchanges leaves at the beginning of and throughout the dry season and stomata of younger leaves are reported to be more responsive in limiting water loss (Reich & Borchert 1988). Regardless of the mechanisms responsible for the seasonal adjustments in g_s of *A. excelsum* and consequent seasonal homeostasis of E , the patterns of behaviour observed were consistent with recent proposals that stomatal regulation of transpiration is based on sensing the transpiration rate itself rather than factors such as V_s or leaf water status (Meinzer & Grantz 1991; Mott & Parkhurst 1991).

Our results suggest that despite relatively low stomatal coupling coefficients ranging from 0.46 during the dry season to only about 0.25 during the wet season, large seasonal adjustments in g_s in combination with seasonal variation in ambient humidity led to seasonal homeostasis of E (Fig. 2b) in *A. excelsum*. The impact of stomatal behaviour on transpiration thus depends on the timescale over which it is being evaluated. During the wet season, for example, relatively large diurnal variations in g_s would be expected to have a small influence on E (Fig. 2b). Similarly, transpiration from a dense, well-irrigated sugarcane canopy was predicted to be nearly independent of diurnal variations in g_s because $1-\Omega$ was only about 0.1 (Meinzer & Grantz 1989). However, large stomatal adjustments during

canopy development in sugarcane caused transpiration to remain nearly constant over a wide range of leaf area index (Meinzer & Grantz 1991).

Results from previous studies suggest that there is considerable variation in g_s and g_{bl} , and consequently, in $1-\Omega$, among tropical tree species. In mixed tropical forest stands, therefore, simultaneous porometric measurements of g_s at the single leaf scale, and of E and total vapour phase conductance in unenclosed branches or entire individuals of dominant canopy species, may constitute a reasonable approach for partitioning control of E between its stomatal and environmental components. The corresponding leaf area index values for each species would be required to scale these measurements to a ground area basis for estimating the influence of species composition on canopy conductance and evapotranspiration. Information of this nature is needed for predicting responses of evapotranspiration to changes in species composition arising from processes such as deforestation and climate change in tropical regions.

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