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## STOMATAL AND BOUNDARY-LAYER CONDUCTANCES IN AN AMAZONIAN TERRA FIRME RAIN FOREST

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### SUMMARY

(1) Diurnal measurements of stomatal conductance ( $g_s$ ) and boundary layer conductance ( $g_a$ ) were made through the canopy at a primary rain forest site in the Amazon Basin, Brazil, in three experimental seasons and over a range of soil water conditions.

(2) Maximum values of  $g_s$  were observed near the top of the 40 m deep canopy and they declined towards the forest floor. Observed values of  $g_a$  also decreased through the canopy, but a slight maximum occurred 20 m from the ground.

(3) In the upper part of the tree canopy the diurnal maximum in  $g_s$  occurred in the mid-morning and the value declined for the remainder of the day. This peak was less marked lower in the canopy, and was not present near the forest floor.

(4)  $g_s$  was correlated negatively with specific humidity deficit ( $D$ ) and positively with solar radiation ( $S$ ). The response of  $g_s$  to  $D$  increased with increasing  $S$  at all but the highest values of  $S$ .

(5) The lowest values of  $g_s$  occurred at the same time as the lowest soil water potentials, although these corresponded to only moderate soil water deficits.

### INTRODUCTION

Complete or partial clearance of tropical forest affects large-scale surface energy balance and carbon dioxide content of the atmosphere, as well as local streamflow and soil stability. Difficulty in assessing the consequence of change in tropical forest cover is exacerbated by a shortage of information on the water, carbon dioxide and nutrient cycles of different forest types (Mooney *et al.* 1980). Detailed studies of such processes serve not only to predict effects of the deforestation, but also to minimize the impact by planting vegetation which matches forest behaviour.

The present research constitutes part of a multidisciplinary study of the energy partition of primary rain forest in the Amazon Basin (Shuttleworth *et al.* 1984a, b; Moore & Fisch 1986). Studies have also been made of rainfall interception by the forest canopy (Lloyd & Marques 1987), of the microclimate above and within canopy, and of soil water content and potential.

This paper considers the spatial and temporal variation of stomatal and boundary layer conductances in the forest canopy.

### MATERIALS AND METHODS

#### *Site*

The central lowland forests of the Amazon region have been described by Takeuchi (1961) and Pires (1978) and consist of three types, varzea, igapo and terra firme forest. Varzea and igapo are low-lying flooded forest types, with greater persistence of flooding

TABLE 1. Details of trees around the meteorological tower, Reserva Ducke, Manaus

Species (Family)	Height (m)	d.b.h.* (cm)	Canopy length (m)
1 <i>Piptadenia suaveolens</i> Miq. (Mimosaceae)†	39.3	79	11.9
2 <i>Licania micrantha</i> Miq. (Chrysobalanaceae)	31.3	39	10.1
3 <i>Bocoa viridiflora</i> (Ducke) Cowan (Caesalpinaceae)	26.2	30	7.3
4 <i>Naucleopsis glabra</i> Spruce ex Baill. (Moraceae)	21.9	17	4.6
5 <i>Enterolobium schomburgkii</i> Benth. (Mimosaceae)	17.4	12	6.4
6 <i>Eschweilera fracta</i> R. Knuth (Lecythidaceae)	11.2	6	5.0
7 <i>Gustavia angusta</i> L. (Lecythidaceae)	11.1	7	6.5
8 <i>Rinorea racemosa</i> O. Ktze (Violaceae)	10.5	5	3.4
9 <i>Scheelea</i> sp. (Araceae)	up to 3		
9 <i>Astrocaryum</i> sp. (Araceae)	up to 3		

\* Diameter at breast height (c. 1.3 m).

† Numbers by species refer to those given in Fig. 1.

for the latter. Terra firme forest occurs on higher ground where there is no surface water and covers 65–70% of the Amazonian area (Pires 1978).

The experimental site was in terra firme forest in the Reserva Florestal Ducke, 25 km from Manaus, Amazonas, Brazil (2°57'S; 59°57'W). The tallest emergent trees were about 40 m high, with the average height of the main tree canopy about 30 m. No distinct layering exists in the canopy in this type of forest and foliage occurred from ground level up to nearly 40 m. Very little litter was present at the base of the trees, and bare soil without a humus layer was a common feature of the forest floor.

A 44 m high sectional aluminium tower was installed in the forest to mount micro-meteorological equipment through and above the forest canopy. Plant physiological measurements were made on foliage accessible from the tower, and on shorter vegetation at ground level within 100 m of the tower.

#### Sampled trees

Eight different trees of different species were accessible from the tower (Table 1, Fig. 1). The ground flora was of the 'Palmeira' type (palms) and sampling concentrated on two common species (Table 1). The results were collected during three experimental sessions, September–October 1983, July–August 1984 and March–April 1985.

#### Stomatal conductance

Measurements of stomatal conductance ( $g_s$ ) were made throughout the forest canopy (Fig. 1) with a diffusion porometer (model AP3, Delta-T devices, Burwell, Cambs., U.K.). Because of the very extensive tree canopy, sampling was only practical by dividing the canopy into two approximately equal height ranges, with a third sample restricted to the ground flora. Each sample portion was investigated on several days during each measurement period, but more sample days were concerned with the upper half of the canopy, and less effort devoted to the ground flora. Four or five sets of measurements, each set consisting of about forty to fifty conductance values, were made throughout the sample day which lasted from about 08.00 to 16.00 hours local time. Determinations were made initially on both the upper and lower leaf surfaces to determine whether to maintain monitoring of both surfaces. In practice, monitoring one leaf surface proved adequate for most species (see Results).

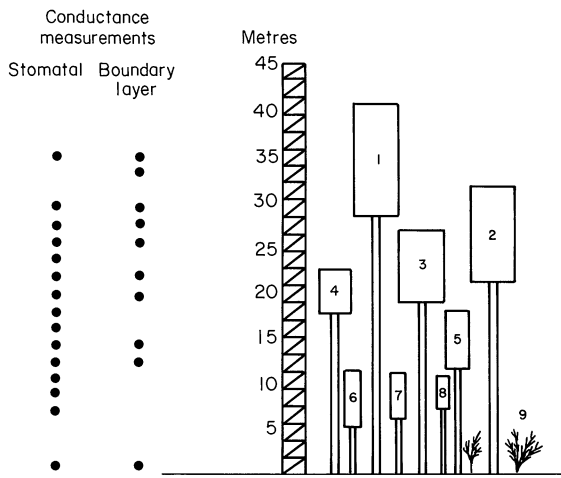


FIG. 1. Schematic representation of trees and palms sampled in the Reserva Florestal Ducke, Manaus and the locations of sampling for stomatal and boundary layer conductances. Table 1 gives a key to the numbers.

The porometer was calibrated before each set of measurements during any day. At the top of the canopy, excessive overheating of the porometer cup was prevented by shading the cup. No progressive closure was observed, suggesting that any shading of the leaf outside the cup was unimportant. However, any residual difference in temperature between porometer and the leaf was corrected for according to the manufacturer's guidelines.

*Boundary-layer conductance*

Boundary-layer conductance ( $g_a$ ) was estimated from the weight loss of wetted leaf replicas using the formula:

$$g_a = E / (X_1 - X)$$

where  $E$  is the water loss rate,  $X_1$  is the specific humidity of air saturated at leaf temperature and  $X$  is the specific humidity of the ambient air. Blotting paper replicas were made of leaves from selected positions throughout the canopy and in the ground flora (Fig. 1). Copies were cut around actual leaves. At each location two wetted replicas were prepared by saturating with water and allowing all excess water to drain off before starting measurements. One of the replicas, of known weight, was weighed at 5-min intervals on a torsion balance and up to five weighings could be made before it dried. The second replica was positioned nearby so that its temperature could be monitored frequently with a bead thermistor (0.75 mm diameter) kept in contact with its under-surface. Absolute humidity in the vicinity of the replica was calculated from wet and dry bulb temperature measured in a double-shielded fully ventilated psychrometer.

*Environmental variables*

Measurements of environmental variables were available from above the forest canopy from two automatic weather stations (Strangeways 1972) which operated continuously during the study. These were mounted at the top of the tower (45 m) and their scanning

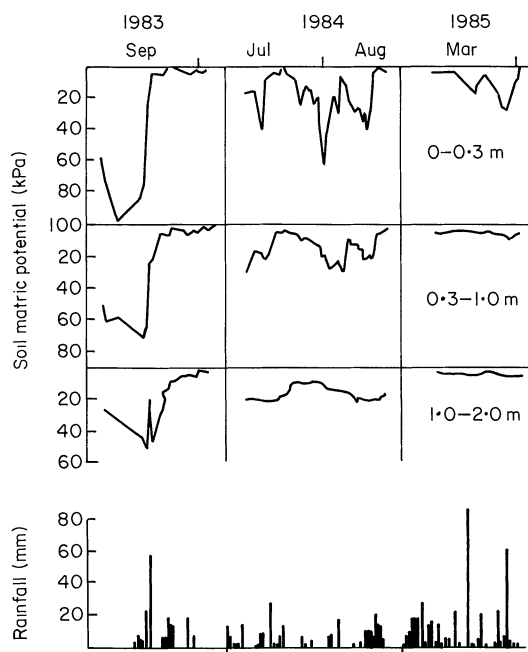


FIG. 2. Rainfall and soil water potential at three soil depths during the three study periods in the rain forest.

interval was 5 min. In addition, more precise data on wet and dry bulb temperatures and windspeeds through and above the forest canopy were obtained from intensive micrometeorological studies simultaneous with the studies reported here (Shuttleworth *et al.* 1985).

#### *Soil water potential*

Soil water conditions 50 m from the tower were monitored using two profiles of mercury manometer tensiometers installed in a depth sequence every 100 mm down to 1 m and then every 200 mm to 2 m.

## RESULTS

### *Rainfall and soil water potential*

The long-term averages for Manaus (Ratisbona 1976) show the wettest months to be January–April, with rainfall then reducing to the driest period from July to September. There is, however, quite large year-to-year variation. Figure 2 shows all aspects of these patterns. The dry period in 1983 followed the long-term trends, and the first soil water data in September 1983 shows this followed by soil water potential rising after storms in the middle of the month. Frequent and heavy rainstorms in the study period spanning March and April 1985 resulted in only small water potentials throughout the soil profile. July and August 1984 were wetter than average and so soil water potentials were less than those observed in September 1983.

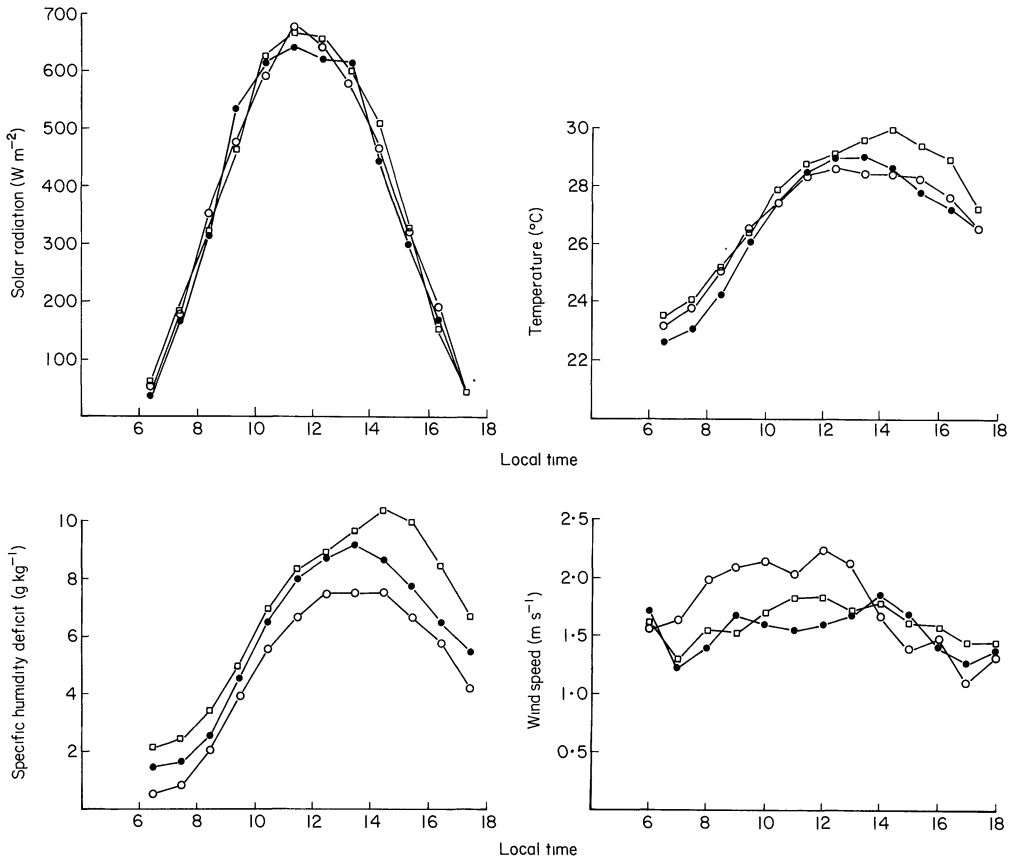


FIG. 3. Hourly averages of solar radiation, temperature, specific humidity deficit and windspeed determined on the days when physiological data were being collected in September 1983 (□), July–August 1984 (●) and March–April 1985 (○).

### *Solar radiation, temperature, humidity deficit and windspeeds*

#### *Above-canopy values*

Figure 3 shows mean diurnal trends of solar radiation, temperature, humidity and windspeed measured above the forest canopy in three study periods for days when physiological measurements were made. Solar radiation was similar for the three periods, but some differences occurred in temperature and, particularly, specific humidity deficit. The highest temperatures occurred in the driest period (September 1983). In the second and third measurement periods the maximum daily temperatures occurred slightly earlier in the day than in September 1983.

The specific humidity deficit data exhibit similar trends to the temperature data, but with a clear distinction between the measurement period of July–August 1984 and that of March–April 1985. Windspeeds were highest in the morning, and this was particularly so in the March–April 1985 period and was probably associated with the frequency of storms at that time.

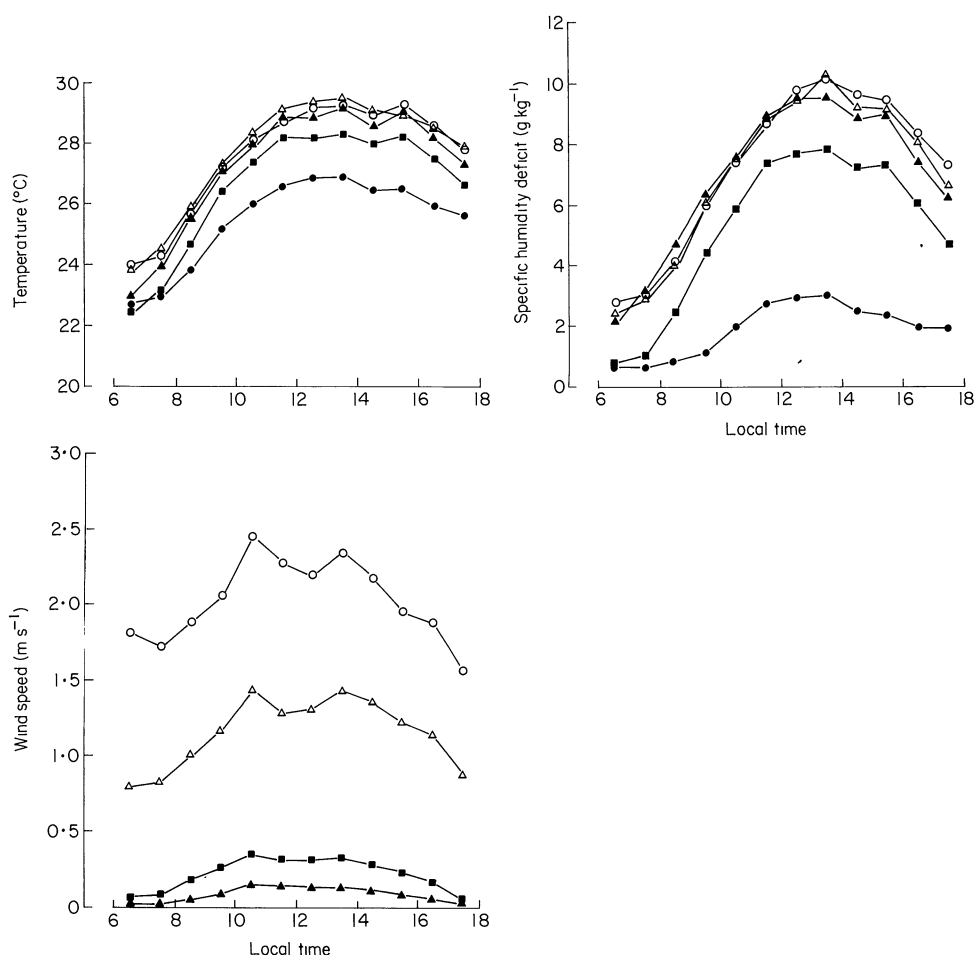


FIG. 4. Hourly averages of temperature, specific humidity deficit and windspeed from measurements made in July–August 1984 at 1.45 m (●), 13.45 m (■), 23.25 m (▲), 35.69 m (Δ) and 44.66 m (○).

### *Within-canopy values*

The micrometeorological equipment within the canopy space was in general not operational until towards the end of the physiological measurements in each study period. However, a very extensive set of data is available for a wide range of conditions from September 1983 to August 1985. Figure 4 shows the hourly average of all the data taken during daylight periods in July and August 1984 at different levels through and above the canopy. A slight depression in temperature and specific humidity deficit occurred around 14.00 h when rainstorms most frequently occurred. A small difference was apparent in the temperature and humidity measured above the forest and those measured in the upper canopy, but most decrease occurred below 23 m. The tree crowns of the emergent and subemergent trees probably intercepted the major fraction of the above-canopy radiation above this level. Windspeed declines markedly through the canopy. Anemometers at the lowest canopy level were stalled almost permanently, suggesting windspeeds below  $0.2 \text{ m s}^{-1}$ .

TABLE 2. Mean stomatal conductances ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) on 5, 6 and 19 September 1983 on lower and upper leaf surfaces of species around micrometeorological tower, Reserva Ducke, Manaus

Species	Lower	Upper	Ratio
<i>Piptadenia suaveolens</i>	233	88	$2.6 \pm 0.12$
<i>Licania micrantha</i>	136	9	$15.1 \pm 1.75$
<i>Bocoa viridiflora</i>	128	15	$8.5 \pm 1.20$
<i>Naucleopsis glabra</i>	72	33	$2.2 \pm 0.54$
<i>Enterolobium schumburgkii</i>	68	47	$1.4 \pm 0.09$
<i>Eschweilera fracta</i>	64	14	$4.6 \pm 0.52$
<i>Gustavia angusta</i>	69	11	$6.3 \pm 0.48$
<i>Rinorea racemosa</i>	69	12	$5.7 \pm 0.60$
<i>Scheelea</i> sp.	81	11	$9.3 \pm 1.43$
<i>Astrocaryum</i> sp.	81	7	$12.0 \pm 1.38$

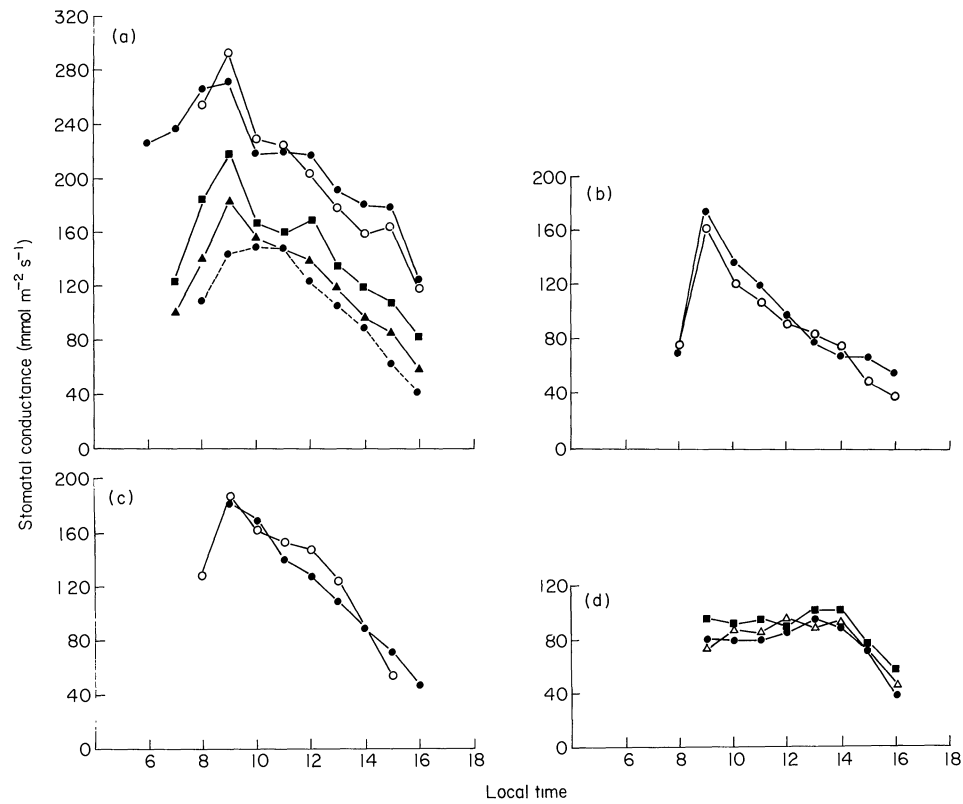


FIG. 5. The diurnal variation in stomatal conductance of the species around the sampling tower, Reserva Florestal Ducke, Manaus. Data points are mean values from all the data for the different species. (a). *Piptadenia suaveolens* at 33 m (●); *P. suaveolens*, 27.5 m (○); *Licania micrantha*, 25.6 m (■); *Bocoa viridiflora*, 24 m (▲); *Naucleopsis glabra*, 20 m (●). (b). *Naucleopsis glabra*, 17 m (○); *Enterolobium schumburgkii*, 13 m (●). (c). *Rinorea racemosa*, 8 m (●); *Gustavia angusta*, 8 m (○). (d). Seedling trees, 0–3 m (■); *Astrocaryum* sp., 0–3 m (●); *Scheelea* sp., 0–3 m (Δ).



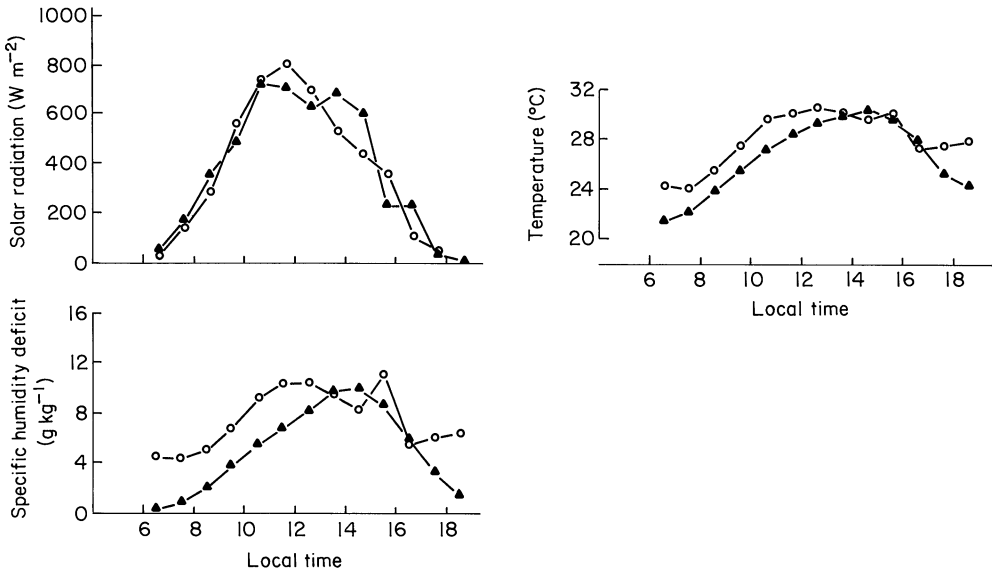


FIG. 6. Changes in solar irradiance, temperature and specific humidity deficit on 7 (O) and 17 (▲) August 1984.

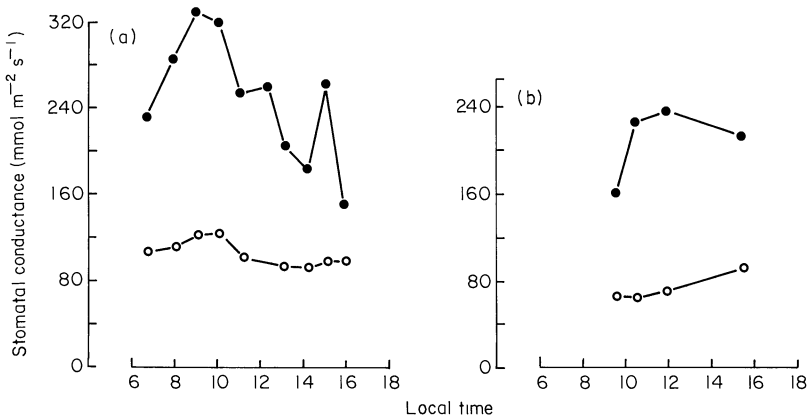


FIG. 7. Diurnal variation in  $g_s$  of upper (O) and lower (●) leaf surfaces of *Piptadenia suaveolens* on (a) 7 and (b) 17 August 1984.

### Stomatal conductance

#### Comparison of upper and lower leaf surfaces

At the beginning of the study, in September 1983,  $g_s$  measurements were made on the upper and lower leaf surfaces in the eight species accessible from the tower and on the two palm species sampled on the forest floor. The ratios of conductances on the lower and upper surface show quite a range of variation (Table 2) but three species had particularly low ratios. Of these, two belonged to the Mimosaceae family.

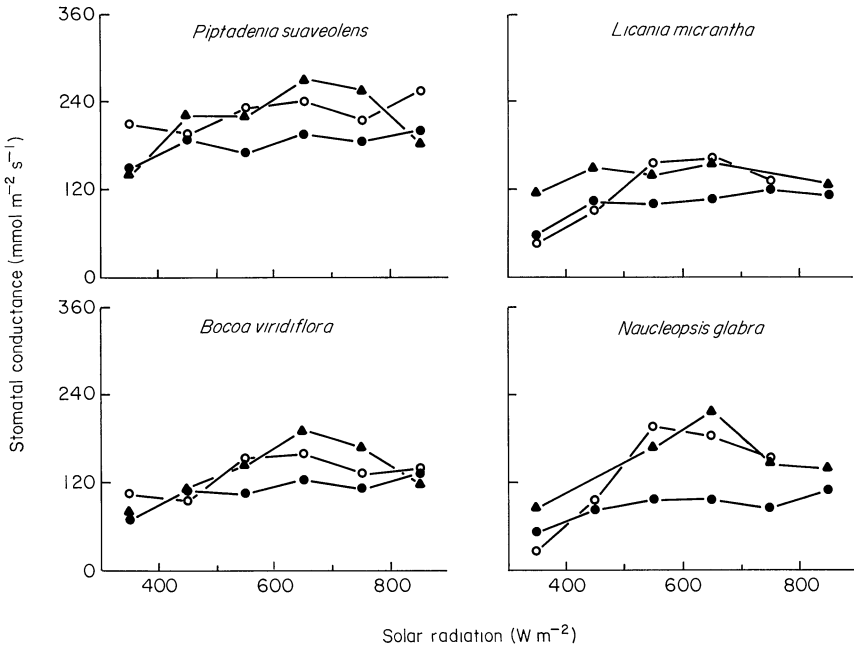


FIG. 8. The relationship of stomatal conductance to above-canopy solar irradiance for four upper canopy species in three study periods, September 1983 (●), July–August 1984 (○) and March–April 1985 (▲).

### Diurnal changes in $g_s$

A consistent pattern of diurnal variation in the values of  $g_s$  for the eight species growing around the tower was found. Values of  $g_s$  rose quite sharply up to around 09.00–10.00 hours and then fell gradually throughout the day (Fig. 5). The trees with crowns in the upper part of the forest canopy had the highest  $g_s$  values and showed the biggest changes after the mid-morning peak. In contrast, plants on the forest floor (mainly palms) had lower  $g_s$  values and exhibited far less diurnal variation. The crowns of trees intermediate between these two extremes had intermediate  $g_s$  values both in magnitude and in diurnal range. Diurnal trends in values of  $g_s$  were associated with variations in daily weather patterns over the forest. Typical responses of stomata in the upper half of the canopy to contrasting environmental conditions are illustrated with data from the emergent tree *Piptadenia suaveolens*. In high radiation conditions, such as those on 7 August 1984, rapid increases in temperature (up to 31 °C) and specific humidity deficit (up to 13 g kg<sup>-1</sup>) (Fig. 6) were associated with a sharp fall in  $g_s$  (Fig. 7). In less demanding conditions of lower solar radiation, temperature and humidity deficit, as on 17 August (Fig. 6), the maximum value of  $g_s$  tended to be lower but the decline in the late morning and afternoon was less pronounced (Fig. 7). The lower leaf surface  $g_s$  seems the more responsive, however.

### Seasonal changes in $g_s$

The values of  $g_s$  have been separated into those collected in each field season as well as into different radiation conditions, by indexing against the solar radiation measured above the forest canopy. Most of the data relate to four species in the upper half of the

TABLE 3. Linear regression statistics for stomatal conductance ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) with specific humidity deficit ( $\text{g kg}^{-1}$ ) in five radiation classes

Above-canopy radiation (W m <sup>-2</sup> )		Species			
		<i>Piptadenia suaveolens</i>	<i>Licania micrantha</i>	<i>Bocoa viridiflora</i>	<i>Naucleopsis glabra</i>
701–800	<i>r</i>	0.55*	0.33 N.S.	0.04 N.S.	0.36 N.S.
	<i>a</i>	459±86	—	—	—
	<i>b</i>	−23.2±8.1	—	—	—
601–700	<i>r</i>	0.55**	0.56**	0.58**	0.70**
	<i>a</i>	327±32	208±26	244±26	271±32
	<i>b</i>	−12.4±3.5	−8.8±2.9	−10.8±2.9	−15.6±3.6
501–600	<i>r</i>	0.65*	0.77**	0.73**	0.73**
	<i>a</i>	310±30	226±22	253±27	309±38
	<i>b</i>	−13.2±3.6	−11.6±2.5	−14.0±3.0	−20.0±4.4
401–500	<i>r</i>	0.77**	0.85**	0.73**	0.80**
	<i>a</i>	313±27	193±19	175±21	185±27
	<i>b</i>	−12.8±2.9	−9.6±2.0	−7.6±2.1	−10.4±2.7
<400	<i>r</i>	0.56*	0.85**	0.72**	0.69*
	<i>a</i>	233±21	137±14	133±15	122±25
	<i>b</i>	−7.6±2.9	−8.0±1.6	−6.0±1.7	−6.8±2.5

*r*, correlation coefficient; *a*, intercept of regression line ( $\pm$  S.E.); *b*, slope of regression line ( $\pm$  S.E.).

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; N.S., not significant.

canopy (Fig. 8). In general,  $g_s$  was lower in all four species in the September 1983 period, but no obvious difference exists between data taken in July–August 1984 and in March–April 1985. Figure 2 shows that soil water potential was lowest when data collection first began in 1983. At that time, at least two of the species, *P. suaveolens* and *Bocoa viridiflora*, had old leaves. In the first of these, a completely new set of leaves emerged the following month and in the second, new leaves were found to have emerged sometime before July 1984.

#### Radiation effects on $g_s$

Figure 8 shows an increase in  $g_s$  for all four upper canopy species, with radiation up to  $600\text{--}700 \text{ W m}^{-2}$ , followed by a levelling off in response. The rise of  $g_s$  with increased radiation was larger in species occurring lower down in the canopy, namely *Naucleopsis glabra* and *B. viridiflora*. However, the radiation actually incident on the leaves of these species was lower, and  $g_s$  for these species will be on a steeper section of the radiation response curve.

#### Humidity deficit effects on $g_s$

To facilitate interpretation of the influence of specific humidity deficit ( $D$ ) on  $g_s$ , the data have again been separated into  $100 \text{ W m}^{-2}$  bands of solar radiation, as measured above the canopy, and the relationship between  $D$  and  $g_s$  then investigated by linear regression analysis. Table 3 presents the coefficients of linear regression for the four species in the upper canopy using data from all three experimental seasons. The regression lines fitted for each species and radiation class are shown in Fig. 9. All species have

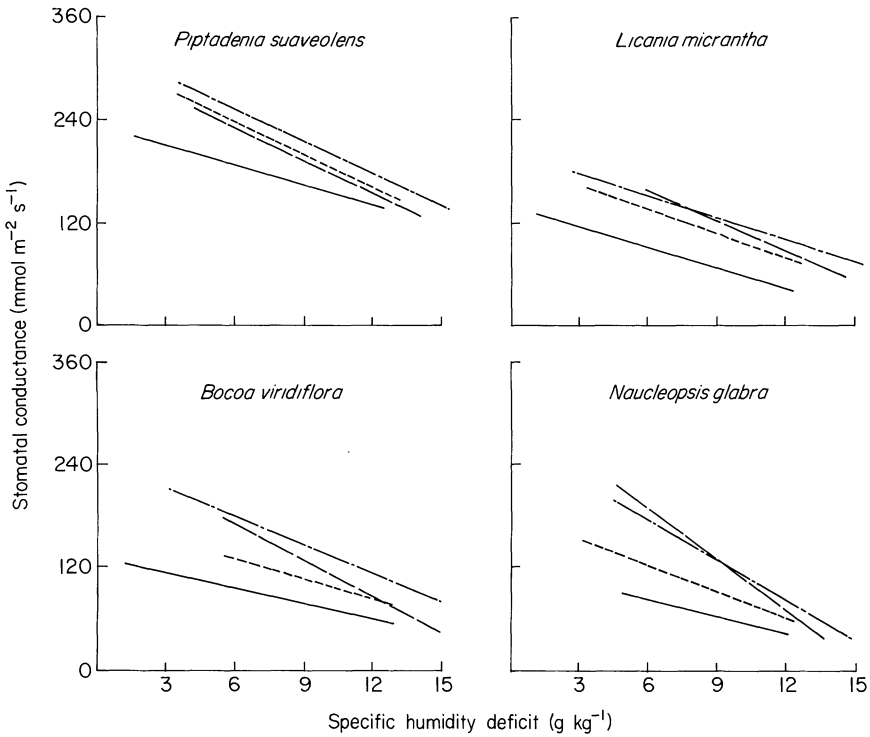


FIG. 9. The relationship between stomatal conductance and specific humidity deficit for four upper-canopy species. Data are pooled from the three study periods but separated depending on above canopy solar radiation conditions:  $<400$  (—),  $401-500$  (---),  $501-600$  (— —) and  $601-700$  (— · —)  $\text{W m}^{-2}$ .

statistically significant negative relationships between  $D$  and  $g_s$  except in the highest radiation class, for which only one species showed a significant relationship. However, there were only a few data in the highest radiation category. Also the slope and intercept increased with increasing radiation and then declined above the  $600 \text{ W m}^{-2}$ .

For periods when sufficient data were available, the relationship between  $D$  and  $g_s$  was examined separately and very high values of  $r^2$  were obtained. The lower values of  $g_s$  in the 1983 period were again apparent. Figure 10 shows the changing relationships between deficit and conductance in *P. suaveolens* for the three periods with a larger response to deficit in March and April 1985. A similar pattern emerged for the other three upper canopy species. The seasonal changes in gradients of  $g_s$  against  $D$  are most marked in the higher radiation classes.

#### Boundary-layer conductance

Figure 11 shows the values of  $g_a$  calculated from data from wetted replica leaves at ten levels through the canopy space. The values of  $g_a$  varied from over  $1400 \text{ mmol m}^{-2} \text{ s}^{-1}$  at the top of the canopy, to  $240 \text{ mmol m}^{-2} \text{ s}^{-1}$  at the forest floor, but higher values were measured at around 10–12 m up from the forest floor than were found at 18–20 m, so that the relationship with height was not linear.

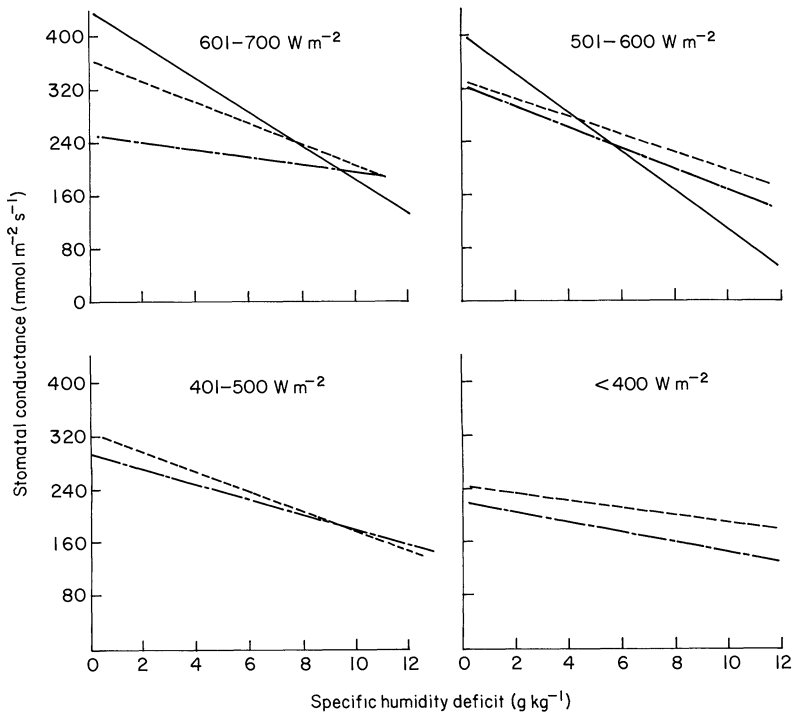


FIG. 10. The relationship between stomatal conductance and specific humidity deficit in four above-canopy radiation classes for *Piptadenia suaveolens*. Data have been separated for each study period, September 1983 (—), July–August 1984 (----) and March–April 1985 (—·—).

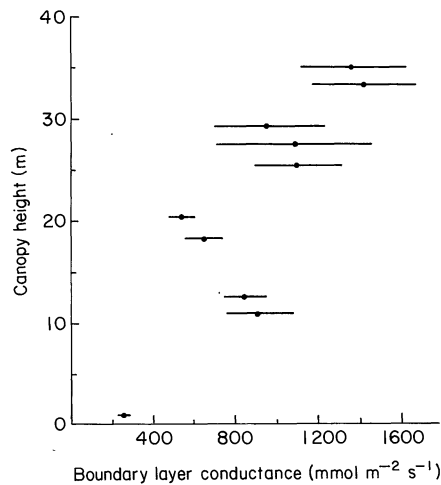


FIG. 11. Variation of boundary-layer conductance with height in the forest canopy. Horizontal bars indicate  $\pm 1$  S.D.

## DISCUSSION

*Forest microclimate*

In temperate forest hydrological studies, Tan, Black & Nnyamah (1978) and Roberts *et al.* (1980) have shown the significant contribution made by the understorey in the forest to the total forest transpiration. Roberts, Wallace & Pitman (1984) found that temperature and specific humidity deficits below the tree canopy in Thetford Forest, East Anglia, seldom differed by more than one unit from the values above the forest in the daylight period. Net radiation below the tree canopy was reduced to about 13% of the above-canopy value, while Oliver (1975) showed that windspeeds were around 10% of those above the forest.

A very different situation was found at this tropical rain forest site. Although only small differences in temperature and humidity deficit were observed between the atmosphere above the forest and in the upper canopy, the foliage of large trees below the emergent layer created steep gradients in temperature and humidity deficit, and differences around midday of about 5 units were not uncommon between the top and bottom of the forest. Shuttleworth *et al.* (1984b) confirmed other reports that solar radiation at the forest floor in tropical forests is around 1% of the above-canopy values (Chazdon & Fetcher 1984). Windspeed, already lower than observed above temperate forests, is reduced at ground level to immeasurable levels, i.e. less than the stalling speed of lightweight cup anemometers used ( $<0.2 \text{ m s}^{-1}$ ). Such gradients of radiation, temperature, specific humidity deficit and windspeed have large effects on the two conductances that influence transpiration loss, namely the stomatal ( $g_s$ ) and the boundary-layer conductance ( $g_a$ ).

*Stomatal conductance**Ranges of stomatal conductance*

Major reviews of  $g_s$  for plants in general (Korner, Scheel & Bauer 1979) and more specifically of the water relations of tropical trees (Doley 1981; Medina 1983) have shown the need for many more data for tropical rain forests. Since these papers, several studies covering a wide range of plant types, species and habitats have been reported, but they do show a wide range in the values of  $g_s$ .

Maximum  $g_s$  values as low as 80 or 100  $\text{mmol m}^{-2} \text{ s}^{-1}$  have been reported for some rain forest tree seedlings (Langenheim *et al.* 1984). Similarly low values were measured by Percy & Calkin (1983) in *Euphorbia forbesii* and *Claoxylon sandwichense*, despite the fact that 1  $\text{mmol m}^{-2} \text{ s}^{-1}$  of photosynthetically active radiation was provided to these understorey plants. Sun & Ehleringer (1986) examined seedlings of *Schima superba* at even higher radiation levels but  $g_s$  was only 140  $\text{mmol m}^{-2} \text{ s}^{-1}$ . These results compare with the values obtained for the ground-level vegetation in this study. In contrast, Mooney *et al.* (1983) showed that *Piper hispidum*, also an understorey plant, had a maximum  $g_s$  as high as 1000  $\text{mmol m}^{-2} \text{ s}^{-1}$ , although its value declined sharply with increasing humidity deficit.

Data for mature trees in upper canopy positions also indicate a wide range of values. Stomatal conductance of *Gmelina arborea* and *Tectona grandis* (teak) in Nigeria was measured in a dry season by Whitehead, Okali & Fasehun (1981), and in a wet season by Grace, Okali & Fasehun (1982). The highest values recorded in the wet season were about 1200  $\text{mmol m}^{-2} \text{ s}^{-1}$  for both species. In the dry season the value of  $g_s$  for *G. arborea* fell to 600  $\text{mmol m}^{-2} \text{ s}^{-1}$ , while for *T. grandis* it had only fallen to 1000  $\text{mmol m}^{-2} \text{ s}^{-1}$ . Grace, Fasehun & Dixon (1980) considered that the low  $g_a$  values of large leaves like those of *T.*

TABLE 4. Transpiration rates ( $\text{mm h}^{-1}$ ) calculated for three canopy levels at four times in a day using the average boundary-layer conductance,  $g_a$  ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) for the canopy level and using higher and lower conductances (in parentheses); the stomatal conductances ( $\text{mmol m}^{-2} \text{s}^{-1}$ ) used are given in square brackets

	$g_a$	Time (hours)			
		06.00	09.00	12.00	15.00
Upper canopy	1400	0.048	0.396	0.470	0.219
	(2000)	0.051	0.365	0.430	0.205
	(800)	0.041	0.440	0.521	0.244
		[220]	[280]	[200]	[160]
Middle canopy	800	0.011	0.149	0.193	0.080
	(1200)	0.011	0.127	0.172	0.073
	(400)	0.010	0.186	0.232	0.098
		[160]	[170]	[140]	[60]
Lower canopy	240	6.77*	7.37*	0.015	0.012
	(360)	7.11*	7.60*	0.017	0.012
	(120)	6.24*	7.03*	0.013	0.011
		[80]	[80]	[80]	[60]

\*  $\times 10^{-3}$

*grandis* would lead to high leaf temperatures, which could be moderated by high transpiration rates with which large  $g_s$  values would be associated. These values of  $g_s$  are not uniquely high amongst tropical trees however. Chiarello (1984) tabulates data from Los Tuxlas, Mexico, for *Urera caracasana* and *Heliocarpus appendiculatus* with maximum values of  $g_s$  of  $1100 \text{ mmol m}^{-2} \text{s}^{-1}$ , while the maximum for *Piper auritum* was 700. Other published values are generally much lower. Aylett (1985), working in a Jamaican upper montane rain forest, found maximum values of  $g_s$  in the upper canopy species of 400 and  $360 \text{ mmol m}^{-2} \text{s}^{-1}$  for a species just below the top of the canopy. These values provide the best comparison with the mean maximum values presented in this paper for foliage at the top of the canopy.

The forest near Manaus was much taller than the forest in Aylett's study which was only 11 m high. Similar  $g_s$  values to those given here are those of Oberbauer, Strain & Reichers (1987) who studied *Pentaclethra macroloba* from ground level to above 25 m in a wet, lowland Costa Rican rain forest. They give maximum  $g_s$  values of only  $160 \text{ mmol m}^{-2} \text{s}^{-1}$  at the highest level but radiation levels were only about a third of maximum daylight values. Understorey plants had  $g_s$  values between 40 and  $80 \text{ mmol m}^{-2} \text{s}^{-1}$ , very similar to the values presented here. Meinzer, Goldstein & Jaimes (1984) excised branches from adult trees of two *Podocarpus* spp. and measured  $g_s$  in an assimilation chamber; low

TABLE 5. The change in the decoupling coefficient,  $\Omega$ , with height in the tropical rain forest canopy

Height (m)	35.7	23.3	13.5	1.45
$\Omega$	0.28	0.26	0.31	0.78

values of  $g_s$  just below  $160 \text{ mol m}^{-2} \text{ s}^{-1}$  were obtained. The two heliophile species which Fanjul & Barradus (1985) studied in a dry tropical forest in Mexico had maximum  $g_s$  values only slightly higher than this.

#### *Influences on stomatal conductance*

The pattern in the values of  $g_s$  and  $g_a$  measured in this study varied consistently through the canopy with the physical environment, suggesting a good prospect for predicting the conductance values for other times in this forest. Values of  $g_s$  declined steadily down through the canopy; trees in higher canopy positions showed a more marked change in  $g_s$  through the day than those lower down. Plant water relations studies (J. Roberts, unpublished) concentrated on *P. suaveolens* and *B. viridiflora*, emergent and subemergent trees, respectively. In July and August 1984, the minimum leaf water potential measured in *P. suaveolens* was close to  $-4.0 \text{ MPa}$  while that in *B. viridiflora* only fell to  $-3.0 \text{ MPa}$ . Under full radiation conditions, in the early afternoon, turgor potentials in the leaves of *P. suaveolens* approached zero in some cases. However, lower in the canopy, lower radiation was associated with lower values of  $g_s$ , and a smaller humidity deficit suggests that stomatal closure is less likely.

Although it is only recently that the response of  $g_s$  to humidity deficit has been investigated for tropical forest vegetation, existing results indicate that many plants show a similar response to those of temperate species. Whitehead, Okali & Fasehun (1981) measured  $g_s$  in *Gmelina arborea* and *Tectona grandis* and both exhibit a decline with increasing  $D$ . In their studies, 80% of the variation in  $g_s$  was accounted for by either radiation or humidity deficit. Mooney *et al.* (1983) found that  $g_s$  in *Piper hispidum* from the lowland tropics of Mexico showed a strong negative response to humidity. A humidity deficit-driven response in  $g_s$  has also been reported for a subtropical species from China (Sun & Ehleringer 1986), while Andrews & Muller (1985) examined leaf gas exchange in the mangrove *Rhizophora stylosa* and found a clear negative correlation between stomatal conductance and both temperature and humidity deficit.

In their study in dry tropical forest, Fanjul & Barradus (1985) showed little response of  $g_s$  to humidity deficit in January when soils were wet, but in April, when soils were drier, a negative correlation was observed between  $g_s$  and  $D$ . In this study the response of  $g_s$  to  $D$  was more sensitive when radiation was high (Fig. 9), but a higher sensitivity was also observed in the March–April period when the soil was wettest. These responses agree well with those shown by Morison & Gifford (1983) who cite other examples and conclude that the sensitivity of stomata to  $\text{CO}_2$  or  $D$  was proportional to the absolute  $g_s$ . More specifically, Morison (1987) examined the  $\text{CO}_2$  response from reports covering twenty-five species and suggested a generalization that the magnitude of the effect of  $\text{CO}_2$  is dependent on the size of  $g_s$ .

There is, however, a possibility that leaf age has an effect in this study, particularly in September 1983 when there was uncertainty about the age of leaves on individual trees, but leaf fall was taking place in *P. suaveolens* and also litter fall was heavy in the forest generally. Borchert (1979) showed that the stomata in 2-month-old leaves of *Tabebuia rosea* in Costa Rica closed when leaf water potentials fell to  $-1.8 \text{ MPa}$ , but 7-month-old leaves did not close their stomata even when the leaf water potential fell to around  $-4.5 \text{ MPa}$ . Additionally, Borchert found that stomatal functioning declined only slowly in the first 5 months, but then did so rapidly. In our study, a lower  $g_s$  was observed with older leaves, but they showed less response to changes in radiation and humidity deficit.



*Boundary-layer conductance*

While there is an accumulating literature on the stomatal conductance of tropical trees, there are still few measurements of the boundary-layer conductance of leaves, the value of which may also have a significant influence on transpiration rate. Grace, Fasehun & Dixon (1980) point out that the balance between the values of  $g_s$  and  $g_a$  can determine the mode of control of transpiration. In this study  $g_a$  was determined throughout the canopy space of the forest and a systematic decline was shown from high values of  $1400 \text{ mmol m}^{-2} \text{ s}^{-1}$  at the top of the canopy down to around 240 at the forest floor.

Grace, Fasehun & Dixon (1980) warn of problems with the determination of boundary-layer conductance using replicas. Calculation of  $g_a$  from the evaporation rate requires an estimate of the vapour pressure at the evaporating surface, and this value is very sensitive to the large variations in temperature that result from differential evaporative cooling and could lead to errors as high as 45%. Table 4 shows the calculations of transpiration using Monteith–Penman formula (Monteith 1965) using average values at four times in the day from July and August 1984 for  $g_s$ ,  $g_a$ , temperature, humidity deficit and net radiation. Only above-canopy net radiation was available and values for the different canopy levels are derived from the above canopy level using a Beer–Lambert Law formulation with an extinction coefficient of 0.6. The effect of changing  $g_s$  and  $g_a$  by  $\pm 50\%$  was also investigated.

At the top of the canopy, a change in  $g_s$  leads to a 30% change in transpiration, but it changes only 10% for a similar change in  $g_a$ . At the base of the canopy, however, the effect of both conductances falls off. Transpiration is very low at the canopy base in any case. Calculations have also been made of the decoupling coefficient,  $\Omega$ , introduced by McNaughton & Jarvis (1983) and Jarvis & McNaughton (1986). This factor describes how well the saturation deficit at the leaf surface is coupled to the air outside the leaf boundary layer; values range from 0, representing very strong coupling, to 1, indicating complete decoupling. Table 5 shows  $\Omega$  calculated for four levels in the rain forest canopy, with a clear gradient from well-coupled at the top of the canopy towards highly decoupled at the forest floor. In this forest, where  $g_a$  values are quite large, the magnitude and behaviour of  $g_s$ , particularly in the upper parts of the canopy, play a key role in determining transpiration. As well as the environmental factors, the other important determinant will be the amount and distribution of leaf area index (L.A.I.) through the canopy space. Unfortunately, good information on L.A.I. for tropical forests is very sparse and there is a need to improve on methods of measuring L.A.I. Measurement of the solar beam transmittance (e.g. Lang, Yuegin & Norman 1985) seems a promising technique which should be assessed in tropical forests.

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