

## Plant Physiological Studies in Tropical Rainforest and Pasture in Amazonia.

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### Abstract

A key parameter in global circulation models is the surface conductance to water vapour transport from vegetated surfaces. Surface conductance integrates over the canopy the influence of individual leaf stomatal conductances. While surface conductance can be measured directly using micrometeorological methods a more detailed understanding of diurnal and seasonal fluctuations requires information about stomatal conductance at the leaf level and its responses to factors which change diurnally and seasonally as well as the magnitude and fluctuations in leaf area index. Therefore basic studies of the plant physiological controls of transpiration involving measurements of leaf gas exchange, plant water relations and leaf area index and its distribution can provide substantial insight on the control of water vapour fluxes at vegetated surfaces.

The Amazonian Regional Micrometeorological Experiment (ARME) and the Anglo-Brazilian Amazonian Climate Observation Study (ABRACOS) were carried out to obtain data to parameterize Global Circulation Models (GCMs) and gain a better understanding of processes at vegetation surfaces which relate to surface climate. Plant physiological studies were part of both of these multidisciplinary experiments.

Seasonal and diurnal patterns of leaf gas exchange and plant water relations as well as leaf area index of rainforest and pasture were compared at three localities in Amazonia: Ji-Paraná in Rondonia, Manaus in Amazonas and at Marabá in Pará. Maximum leaf conductances,  $g_{smax}$ , in all three forests were broadly similar, around  $450 \text{ mmol m}^{-2} \text{ s}^{-1}$ , and there were similar patterns of change from the maximum values.  $g_{smax}$  fell systematically down through the forest canopies to values of around  $50\text{-}100 \text{ mmol m}^{-2} \text{ s}^{-1}$ . Peak values were usually observed around mid-morning and fell steadily during the day. At all of the forest sites there was a negative correlation between air humidity deficit ( $D$ ) and stomatal conductance,  $g_s$ , and the slope of the relationship is less in conditions where  $g_s$  is lower initially such as at lower levels of solar radiation and at the base of the rainforest canopy. Only at the Marabá site and only for a limited number of species is there any indication that soil moisture deficits are influencing stomatal conductance in forests. Although leaf water potential,  $\psi$ , fell to as low as  $-4.0 \text{ MPa}$  at the top of the forest canopy there is no good correlation between  $\psi$  and  $g_s$  and incident radiation and  $D$  are thought to be the major controls. Leaf area index,  $L^*$ , of the forests was around 6 at Manaus, 5.3 at Marabá and 4.4 at Ji-Paraná.

A multi-layer model of forest transpiration based on the Monteith-Penman equation has been formulated which incorporates the stomatal conductance functions and leaf area index information from the Manaus forest site, the Reserva Ducke. The model, CLATTER, predicts daily transpiration values close to those measured with an eddy correlation device. The model shows that because of lower conductances and less demanding microclimate at positions lower in the canopy the equivalent amount of leaf area index is less effective than higher in the canopy.

$g_{smax}$  at all the pasture sites was higher than at the forest sites. However the responses to changing conditions were different for pasture compared to forest and differed more between sites. At Ji-Paraná the pasture was *Brachiaria brizantha*, at Manaus *B. decumbens* and *B. humidicola* and *Panicum maximum* was the predominant species in the Marabá pasture. At Ji-Paraná and Manaus  $g_s$  fell in response to soil moisture deficits but at Marabá there was little evidence of this response. No relationship between  $g_s$  and  $D$  were found at Manaus or Ji-Paraná but a significant negative relationship was found at Marabá. Maximum  $L^*$  (all vegetation) was highest at Ji-Paraná  $\sim 3.8$  and below 2 at Marabá. However seasonal changes are much more substantial at Marabá with a value of only 0.5 at the end of the dry season. At Marabá it seems that reduction in transpiration from the pasture is mostly a function of reduction in leaf area but at Ji-Paraná both lowering of  $g_s$  and  $L^*$  play a role.

## Introduction

A key parameter in global circulation models is the surface conductance to water vapour transport from vegetated surfaces. Surface conductance integrates over the canopy the influence of individual leaf stomatal conductances. While surface conductance can be measured directly using micrometeorological methods a more detailed understanding of diurnal and seasonal fluctuations requires information about stomatal conductance at the leaf level and its responses to factors which change diurnally and seasonally as well as the magnitude and fluctuations in leaf area index. Therefore basic studies of the plant physiological controls of transpiration involving measurements of leaf gas exchange, plant water relations and leaf area index and its distribution can provide substantial insight on the control of water vapour fluxes at vegetated surfaces.

This paper examines, specifically, physiological studies carried out during ten years of collaborative Anglo-Brazilian research. Plant physiology studies are carried out within the framework of multi-disciplinary studies with their scope ranging from climate measurements to studies of soil water processes. Initially in the ARME (Amazonian regional micrometeorological Experiment) project (Shuttleworth et al 1984a and b, 1985) the focus was on defining the surface energy budget, heat fluxes and their controls at one rainforest site in the central Amazon near Manaus. More recently in the ABRACOS (Anglo-Brazilian Amazonian Climate Observation Study) project (Gash et al 1995) attention has been turned to the impact of deforestation on surface climate and comparative studies have been made at three paired forest and pasture sites in Amazonia. Detailed physiological studies have been carried out at all six ABRACOS sites within both the ARME and ABRACOS projects.

The principal aims of plant physiological studies in this context are firstly, to acquire detailed understanding of processes controlling transpiration from vegetation at both forest and pasture sites which would facilitate understanding and modelling of data sets acquired by other measurement disciplines namely micrometeorology and soil water physics. These latter types of measurement integrate over larger areas and over the whole height profile of vegetation but offer less scope than physiological studies to define functional relationships and to identify sources of transpiration flux within complex rainforest canopies. This paper overviews the range of plant physiological studies carried out in Amazonia drawing out the major conclusions and notable similarities and differences which might exist between vegetation types and localities. The relevance of some of the results emerging from these studies to current thinking in ecophysiology and global ecology are assessed. Finally the paper considers directions that plant physiological research in rainforests and replacement vegetation should take in future years.

## Materials and Methods

### *Sites and vegetation*

To gain some insight into the regional variation of the climate and soil water conditions and aspects of the micrometeorology and plant physiology, experimental sites were established in three different areas of Brazil (Figure 1, Table 1). The forest site Reserva Ducke and the ranch land site Fazenda Dimona are located near Manaus in central Amazonia. The forest site Reserva Vale do Rio Doce and the ranch land site are near Marabá in Pará in the eastern Amazon, while the forest site Reserva Jaru and the ranchland site Fazenda Nossa Senhora da Aparecida are located Ji-Paraná in Rondonia in the western Amazon. An analysis of rainfall patterns in the Amazon region by Figueroa and Nobre (1990) shows December to April as the wettest period in all these three areas and the dry season is regarded as lasting from June until August. Although the rainfall at all of the sites has these general characteristics, there are important differences between the sites. Manaus has the wettest conditions, and although the period from June to August is drier than the rest of the year, there is still a substantial amount of rainfall. The dry season at Ji-Paraná and at Marabá is more pronounced than at Manaus, and there are often several weeks without rainfall. Figure 2 shows the long term average monthly rainfall from climatological stations close to the ABRACOS sites.

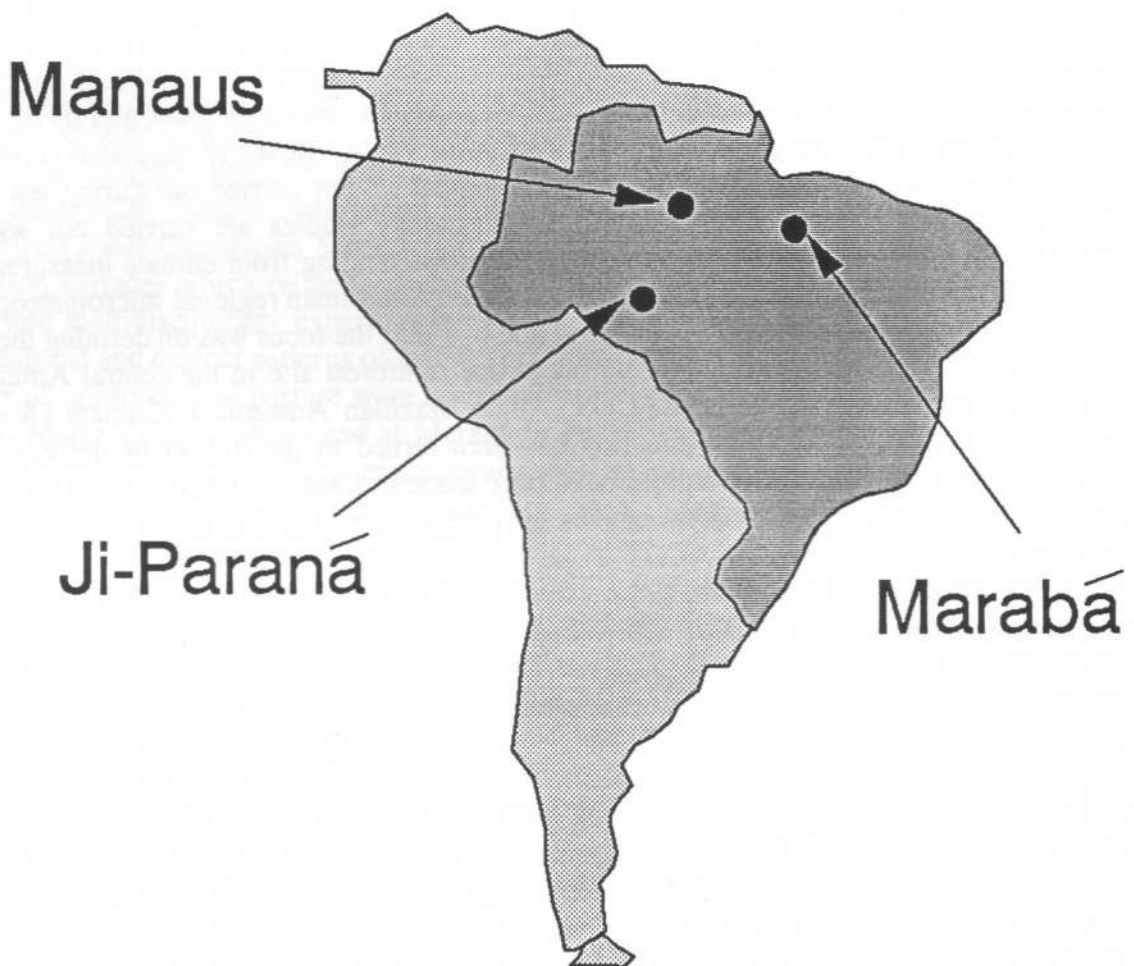


Figure 1. Brazil showing the location of the ARME and ABRACOS sites.

Site	Location	Vegetation	Established	Coordinates
Reserva Vale do Rio Doce, Pará	Marabá	Tropical Forest	July 1991	5°45'S,49°10'W
Fazenda Boa Sorte	"	<i>Panicum maximum</i> , Shrubs.	July 1991	5°10'S,48°45'W
Reserva Ducke	Manaus, Amazonas	Tropical Forest	September 1990	2°57'S,59°57'W
Fazenda Dimona	"	<i>Brachiaria decumbens</i> , <i>B. humidicola</i> , shrubs.	September 1990	2°19'S,60°19'W
Reserva Jaru	Ji-Paraná, Rondônia	Tropical Forest	October 1991	10°05'S,61°55'W
Fazenda Nossa Senhora	"	<i>Brachiaria brizantha</i>	October 1991	10°45'S,62°22'W

**Table 1:** The ABRACOS sites.

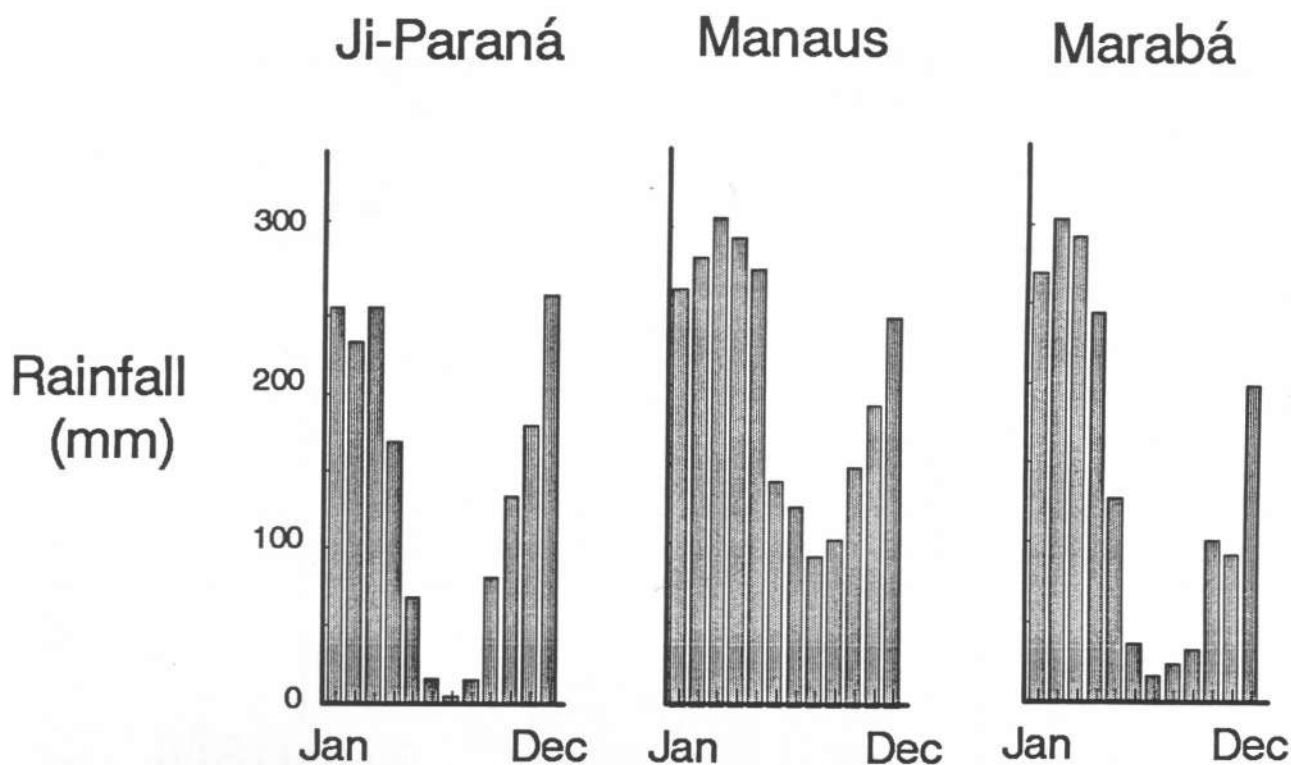


Figure 2. Average monthly rainfall for the three ABRACOS sites, Ji-Paraná, Rondonia; Manaus, Amazonas and Marabá, Pará.

Automatic weather stations (AWS) were installed at both forest and clearing sites at the three locations in the study. At each of the forest sites the AWS is located at the top of a sectional aluminium towers reaching to a few metres above the top of the forest canopy. At the clearing sites the AWS is located at ground level (Manaus) or at the top of a 6 m tower (Marabá and Ji-Paraná). Each AWS is equipped with a range of instruments the data from which is recorded as hourly averages from samples made every 10 seconds using solid state loggers (Campbell Scientific, Shepshed, UK). The instrumentation consisted of upward and downward facing pyranometers measuring incoming and reflected radiation, a net radiometer, soil heat flux plate, shielded and aspirated wet and dry bulb thermometers, windspeed and direction and rainfall are also measured. Further details of each of the forest and pasture sites follow.

#### *Reserva Ducke, Manaus*

Reserva Ducke ( $2^{\circ}57'S, 59^{\circ}57'W$ ) is a reserve of primary forest, 25 km northeast of Manaus at 80m above mean sea level. The soil here is classified as a xanthic ferrasol in the FAO terminology and the surface soil texture is clay. The experimental site was the site of the Amazonian Regional Micrometeorological Experiment at the beginning of the 1980s (Shuttleworth et al., 1984) but was reinstated for ABRACOS in 1990. The mean forest canopy is 35 m high, but some trees reach up to 40 m. The tallest species in the area around the tower are *Piptadenia suaveolens* Miq., *Licania micrantha* Miq., *Bocoa viridiflora* (Ducke) Cowan,



*Naucleopsis glabra* Spruce ex Baill, and *Enterolobium schomburgkii* Benth. Undisturbed forest surrounds the forest for a distance of at least 5 km.

#### *Fazenda Dimona, Manaus*

Fazenda Dimona (2°19'S, 60°19'W) is a cattle ranch located about 100 km north of Manaus. The soil has the same classification as the Reserva Florestal Ducke. The ranch is a 10-km<sup>2</sup> clearing at an altitude of 120 m above mean sea level. It was created over 12 years ago by felling and burning primary forest. The pasture grasses *Brachiaria decumbens* and *B. humidicola* were planted, but 11 per cent of the ground area is bare soil and many felled tree trunks still remain, covering 5 per cent of the ground (Wright et al., 1992).

#### *Reserva Vale do Rio Doce, Marabá*

This forest site (5°45', 49°10'W) was established in July 1991 in the forest reserve of the Companhia Vale do Rio Doce, 50 km to the south of Marabá. The forest reserve is 17 000 hectares in area and largely undisturbed but almost completely surrounded by cleared areas. The soil at the forest reserve is classified as a humic cambisol with a loamy surface texture. The automatic weather station is mounted on top of a 52-m tower positioned to the east of a mature Brazil nut tree (*Bertholletia excelsa* HBK) with a height of 49 m. However the continuous forest canopy consisting mainly of *Inga alba* (SW) Willd, *Pouroma guianensis* Aubl., *Guarea guidonia* (L.) Sleumer, and *Sagotia brachysepala* (Muell Arg.) R. Secco surrounding the tower was substantially lower at around 20-25m. Further details of the species at the forest site can be found in Sá et al (1995). The presence of very large Brazil nut trees is a characteristic of forests of this region. Further details of the floristics of this forest reserve can be found in Salomão (1991).

#### *Fazenda Boa Sorte, Marabá*

Fazenda Boa Sorte (5°10'S, 48°45'W) is a cattle ranch 50 km to the northeast of Marabá at 170 m above mean sea level. The site was established in July 1991 and is a large area of pasture dominated by *Panicum maximum* Jacq. with associated babaçu palms (*Orbignya phalerata*) and miscellaneous shrubs. The soil is classified in the FAO terminology as an orthic Acrisol and has a surface texture of sandy clay loam. Further details of the vegetation can be found in Sá et al., (1995).

#### *Reserva Jaru, Ji-Paraná*

Reserva Jaru (10°05'S, 61°55'W) is a forest reserve administered by IBAMA and is located about 80 km north of Ji-Paraná at 120 m above sea level. The surface soil texture is sandy and classified as an orthic Acrisol in the FAO scheme. A 52-m forest tower was installed in October 1991. The mean height of the canopy is 33 m. The tallest tree species in the area immediately surrounding the tower are *Cedrella odorata*, *Inga* spp, *Dioclea bicolor* Bth, *Strychnos amazonicus* Krukoff, *Protium polybotrium* and *Leonia glyxicarpa* Ruiz. Further details of the forest structure are given by McWilliam et al. (1995).

*Fazenda Nossa Senhora da Aparecida, Ji-Paraná*

This site (10°45'S, 62°22'W) was established at a cattle ranch 220 m above sea level about 50 km east-northeast of Ji-Paraná. The soil is a loamy sand classified as an orthic Acrisol. The site was deforested about 14 yr ago and is in the centre of an area of about 50 km in radius that has been almost completely cleared. The pasture grass at the fazenda is *Brachiaria brizantha* and is still clumpy which reflects the original planting rows. In April 1993 around 12 per cent of the area was bare soil. There are a few palms here as at Fazenda Boa Sorte and very few dead tree trunks remain.

*Leaf area index - forest (L\*)**Manaus*

For the Manaus forest site there are three separate estimates of  $L^*$ . (1)  $L^*$  and its vertical distribution was measured using destructive sampling in a 400 m<sup>2</sup> plot in September and October 1990 (McWilliam et al., 1993). (2) Roberts et al. (1993) assumed that average leaf life span was 12 months and that therefore the annual cumulative litter leaf area equates to the canopy  $L^*$ . Litter leaf area measurements were made at the Reserva Florestal Ducke over a two-year period from 1983 to 1985. Over this period litter was collected at approximately two-weekly intervals in 20 trays with bases perforated for drainage (0.11 m<sup>2</sup>). Area was measured with a leaf area machine (Li-3100, Licor Inc, Lincoln, USA). (3) Another approach adopted by Roberts et al. (1993) was to calculate the vertical distribution of leaf area from published information from the Manaus area (Klinge, 1973; Klinge et al., 1975). Conversion of this published information of vertical distribution of leaf fresh weight to leaf area required assumptions about leaf fresh weight to dry weight ratios and the specific leaf area appropriate to canopy layers (Medina and Klinge, 1983).

*Marabá*

Litter collections have also been made at the Reserva Vale do Rio Doce, Marabá for three years beginning in August 1991. 18 litter collection trays (0.34 m<sup>2</sup>) were used and litter was collected at fortnightly intervals. Total area of the foliage portions of the litter collected in each tray was measured with a leaf area machine (Li-3100, LICOR Inc., Lincoln, Nebraska, USA). Total dry weight of leaf litter in each tray was also determined. A close relationship was found between litter leaf area (m<sup>2</sup>) and dry weight (kg) at Marabá in data pooled from all litter trays for all the bi-weekly samples over the period when these data are available (August 1991 to January 1993). The regression equation

$$\text{area} = -1.58 + 8.49 \text{ weight} \quad (r^2 = 0.977)$$

can serve as a good estimator of litter leaf area from leaf litter weight only. Since December 1992 in addition to total leaf area and dry weight in each tray individual leaves had their area and dry weight determined to derive specific leaf area,  $\delta_f$ , (m<sup>2</sup> kg<sup>-1</sup>). In June and December 1992 samples of healthy fully expanded foliage for each species accessible from the towers at Marabá were selected. The area of each leaf was measured with a leaf area machine and the oven dry weight obtained and  $\delta_f$  calculated for each leaf.

*Ji-Paraná*

Litter collections were made for 12 months beginning in July 1992 using similar trays to those at Marabá and also collecting at two week intervals. Area measurement used a leaf area measurement system (Delta-T Devices, Cambridge, UK).

*Leaf area index - pasture*

Sampling was done at Fazenda Dimona, Manaus in 1990, at Fazenda Nossa Senhora da Aparecida, Ji-Parana and Fazenda Boa Sorte, Maraba in 1992 and 1993. At each sampling occasion twelve plots of grass and shrubs (above-ground parts only) were sampled randomly in the clearing areas using a 0.5 or 1 m<sup>2</sup> quadrat. The total fresh weight of the samples was measured, and a measured ten per cent sample taken. This subsample was divided into living and dead material and the living material further subdivided into stem and leaf material. Leaf area and biomass were measured as for the forest samples.

*Stomatal conductance ( $g_s$ )*

Table 2 summarises the timing and equipment used for measurements of  $g_s$  at the various sites in the ARME and ABRACOS experiments. On each sample day measurements usually commenced around 0800 hours local and were made every two hours until 1600 hours. Further details such as numbers of samples will be found for the Manaus forest in Roberts et al., 1990; for the Ji-Paraná forest and pasture in McWilliam et al., 1995 and for the Marabá forest and pasture in Sá et al., 1995. When an infra red gas analyser was used to measure  $g_s$  as in the case of Ji-Paraná forest and pasture leaf photosynthesis measurements were also made.

*Leaf water potential ( $\psi$ )*

Logistics prevented  $\psi$  being measured at the Marabá pasture site and only a limited amount of data was collected at the Reserva Florestal Ducke. This information is also summarised in Table 2. Measurements were made with a Schölander type pressure chamber (Schölander et al., 1965) around the same times that  $g_s$  was measured. All precautions were taken to prevent evaporation from the samples by wrapping the sampled leaves in "cling film" and transporting them to the pressure bomb in a plastic box lined with wet paper.

*Boundary-layer conductance*

These measurements have only been made at the Reserva Florestal Ducke, Manaus and the Reserva Vale do Rio Doce, Marabá. 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 deficit 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 the ground flora. 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 with up to five weighings being made while the whole replica



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Manaus Forest, Reserva Florestal Ducke

Equipment: Model AP3, Delta-T Devices, Cambridge, UK

Scholander pressure chamber, IH, Wallingford, UK

September/October 1983    July/August 1984    March/April 1985

g <sub>s</sub>	-	-	-
ψ	-	-	-

Manaus Pasture, Fazenda Dimona

Equipment: Infra-red gas analyser, Model LCA3, ADC, Hoddesdon, UK

Scholander Pressure Chamber, IH, Wallingford, UK

September/October 1990    July/August 1991

g <sub>s</sub>	-	-
ψ	-	-

Ji-Paraná Forest, Reserva Jaru and Ji-Paraná Pasture, Fazenda Nossa Senhora da Aparecida

1992                      April 1993                      July 1993

g <sub>s</sub>	-	-	-
ψ	-	-	-

Marabá Forest, Reserva Vale do Rio Doce and pasture Fazenda Boa Sorte.

11 measurement missions between August 1991 and October 1993 using a Model AP4, Delta-T Devices, Cambridge, UK for g<sub>s</sub> and for ψ in the forest only a Scholander Pressure Chamber, IH, Wallingford, UK. Measurement periods were: August and November 1991, January and December 1992,

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Table 2 : Timing and equipment used in plant physiology measurements

surface was wet. The second replica was positioned nearby and its temperature could be monitored frequently with a bead thermistor (0.75 mm diameter) kept in contact with its undersurface. Absolute humidity in the vicinity of the replica was calculated from wet and dry bulb temperature measured with a double-shielded fully ventilated psychrometer.

### *Within-canopy microclimate*

Measurements of temperature, humidity deficit and windspeed have been made through and above the canopies at all three rainforest sites. Here only the set up at the Reserva Florestal Ducke is referred to. A description of the instrumentation and some interpretations have already been given by Shuttleworth et al (1985) and Roberts et al (1993). The data used comes from instrumentation located at 1.45, 13.45, 23.25, 35.69 and 44.66 m above ground level. The highest of these levels was above the tallest trees.

### *Micrometeorology*

The micrometeorological instrumentation used to derive evaporative fluxes from clearing vegetation has been fully described by Wright et al. 1992 and consisted primarily of a vertical profile of logarithmically-spaced shielded and aspirated wet and dry bulb thermometers and fast-response anemometers mounted on a 9 m sectional aluminium tower. Fluxes of latent and sensible heat were derived from the profile of temperature and humidity. Four net radiometers at the top of the tower and soil heat flux plates buried 10 mm below the soil surface provided estimates for the available energy. The profile of vertical windspeed was used to derive aerodynamic properties for the pasture vegetation. The instrumentation was supplemented by direct measurement of the latent and sensible heat fluxes using an eddy correlation device "Hydra" developed at the Institute of Hydrology. Further data were available from a Bowen ratio equipment measuring gradients of temperature and humidity above the clearing (Campbell Scientific, Shepshed, UK). The profile and Bowen ratio methods are not appropriate for measurements over forests because of the very small gradients of temperature and humidity and only data from the eddy correlation device was used. In the case of the central Amazon forest at Manaus it was necessary to draw on earlier information made over the forest using an earlier form of the "Hydra" Shuttleworth et al. 1984. Later studies at the Ji-Paraná and Marabá sites involved deploying the "Hydra" above the forest sites also.

### *Soil Water*

Changes in soil water content in forested and cleared sites at the three locations in the ABRACOS experiment are monitored at approximately weekly intervals using a neutron probe (Didcot Instrument Co., Abingdon, UK). These measurements were made at 10 cm depth intervals in at least six neutron probe access tubes at each site. Each tube penetrated to a depth of 3.6 m except in the case of some tubes in the forest at Ji-Paraná where bedrock prevented this.

## The Multi-layer Transpiration Model

### Model Framework

Total transpiration ( $T$ ) for the forest canopy was estimated by summing calculated fluxes given by the Penman-Monteith formulation, viz

$$\lambda T_i = \frac{\Delta'_i (R_{n,i-1} - R_{n,i}) + \rho c_p (\delta q_i) g_{a,i}}{\Delta'_i + (c_p/\lambda) (1 + g_{a,i}/g_{c,i})} \quad (1)$$

applied at each of the five levels in the canopy. In the above equation

- $R_{n,i-1} - R_{n,i}$  is the radiative energy absorbed by the  $i^{\text{th}}$  layer of the forest;
- $c_p$  is the specific heat of air at constant pressure;
- $T_i$  is the canopy layer transpiration rate;
- $g_{a,i}$  is canopy layer boundary-layer conductance;
- $g_{c,i}$  is canopy layer stomatal conductance;
- $\delta q_i$  is canopy layer specific humidity deficit;
- $\Delta'_i$  is the rate of change of saturated specific humidity with temperature at the canopy layer;
- $\lambda$  is latent heat of vaporisation of water and
- $\rho$  is density of air.

The set of equations are identified throughout this paper by the name CLATTER (canopy layer and total transpiration estimation routine).

Following Landsberg (1986), the net radiation beneath the  $i^{\text{th}}$  layer in the forest canopy is approximated by the Beer-Lambert Law,

$$R_{n,i} = R_{n,o} \exp \left\{ -k \sum_{j=1}^i L_j^* \right\} \quad (2)$$

where:

- $R_{n,i}$  = the radiation beneath the  $i^{\text{th}}$  canopy layer
- $R_{n,o}$  = the net radiation above the canopy
- $k$  = an extinction coefficient (taken here as 0.6)
- $L_j^*$  = leaf area index of layer  $j$  (where  $j = 1$  to  $i$ ).

This value of  $k$  combined with the  $L^*$  data presented below estimated a residual net radiation at the forest floor of 2.5 per cent wholly consistent with measurements made in that position in this forest by Shuttleworth et al. (1984b).

For each of the canopy layers stomatal conductance, ( $g_c$ ) was calculated from:

$$g_{c,i} = L_i^* \cdot g_{s,i} \quad (3)$$

where:

$$\begin{aligned} L_i^* &= \text{the leaf area index of a given canopy layer and} \\ g_{s,i} &= \text{the leaf stomatal conductance a given canopy layer.} \end{aligned}$$

Leaf boundary-layer conductances made in individual canopy layers were scaled up in exactly the same way to give a canopy layer conductance.

## Results

### *Leaf area index - forest*

Figure 3 shows the cumulative litter leaf area index for three years at Marabá and indicates the consistency in amounts falling each year with slight peaks of fall around August and September in the dry season. Table 3 summarises the various estimates of leaf area index for the three ABRACOS sites. Although various methods have been used to measure and estimate leaf area index and a number of assumptions have been made there is overall consistency in the estimates for each site. The estimate for forest at Manaus derived by Roberts et al., (1993) from data published by Klinge (1973) and Klinge et al., (1975) is higher than the other two estimates particularly that of McWilliam et al., (1993). It may be relevant that these last authors sampled in September and October 1990, the dry season at Manaus when the canopy quantity should be least. The use of leaf fresh weight to derive estimates of leaf area should be used with caution because of the potential differences in fresh:dry weight ratio depending on the water content at the time of sampling. The fresh weights of foliage given by McWilliam et al. (1993) for Manaus in the central Amazon which was equivalent to a  $L^*$  of 5.7 which was 1.09 times the  $12.9 \text{ t ha}^{-1}$  which Higuchi et al. (1994) measured in Southern Pará, also close to Marabá. Using these values it can be estimated that the  $L^*$  for Higuchi et al's plot was 5.3 identical to the average of the values estimated from litter leaf areas for the ABRACOS Marabá site. At Ji-Paraná there was excellent agreement between the estimate from litter fall and the gap fraction method used by Grace (Table 3). Overall, these estimates indicate a difference between sites with the Reserva Ducke at Manaus having around 35 per cent more foliage than the forest at Ji-Paraná and about 15 per cent more than at the Marabá forest site.

There is much less information about the vertical distribution of  $L^*$  for the ABRACOS sites with the only direct measurements being those described by McWilliam et al (1993). Figure 4 shows good correspondence between the downward cumulative values determined by McWilliam et al compared with estimates made by Roberts et al (1993) from literature values of Klinge (1973) and Klinge et al., (1975). The vertical distribution of the foliage is important to multi-layer canopy transpiration modelling and we return to it later in discussions of effective leaf area index.

Marabá, Litter Leaf Area Index, 1991-1994

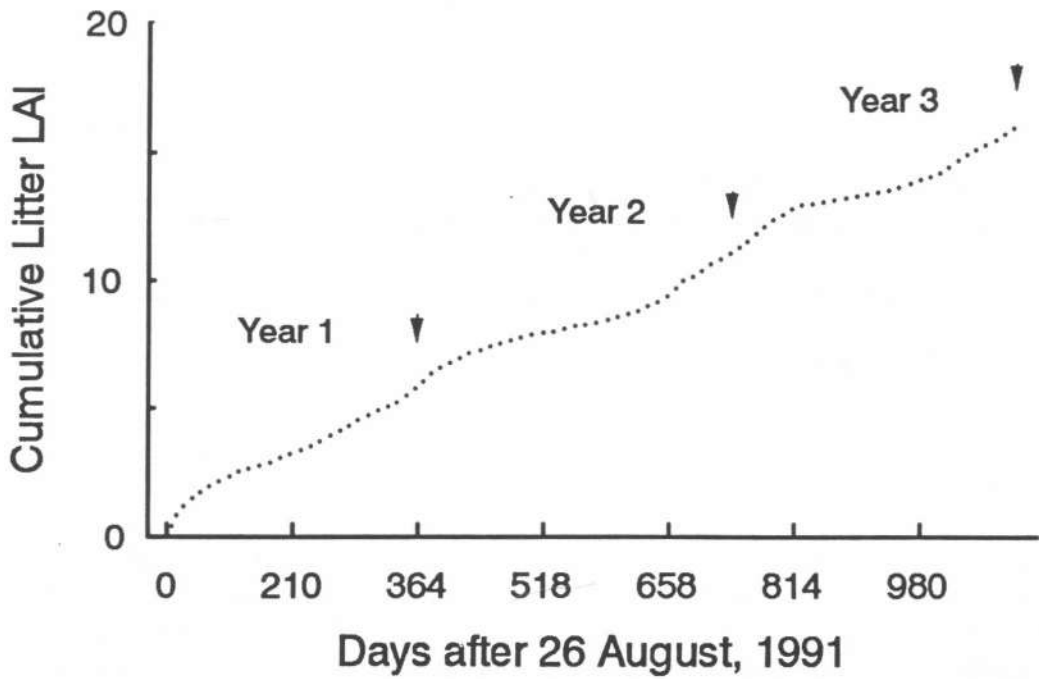


Figure 3. Cumulative leaf litter area index for three years from August 1991 at the Reserva Vale do Rio Doce, Marabá.

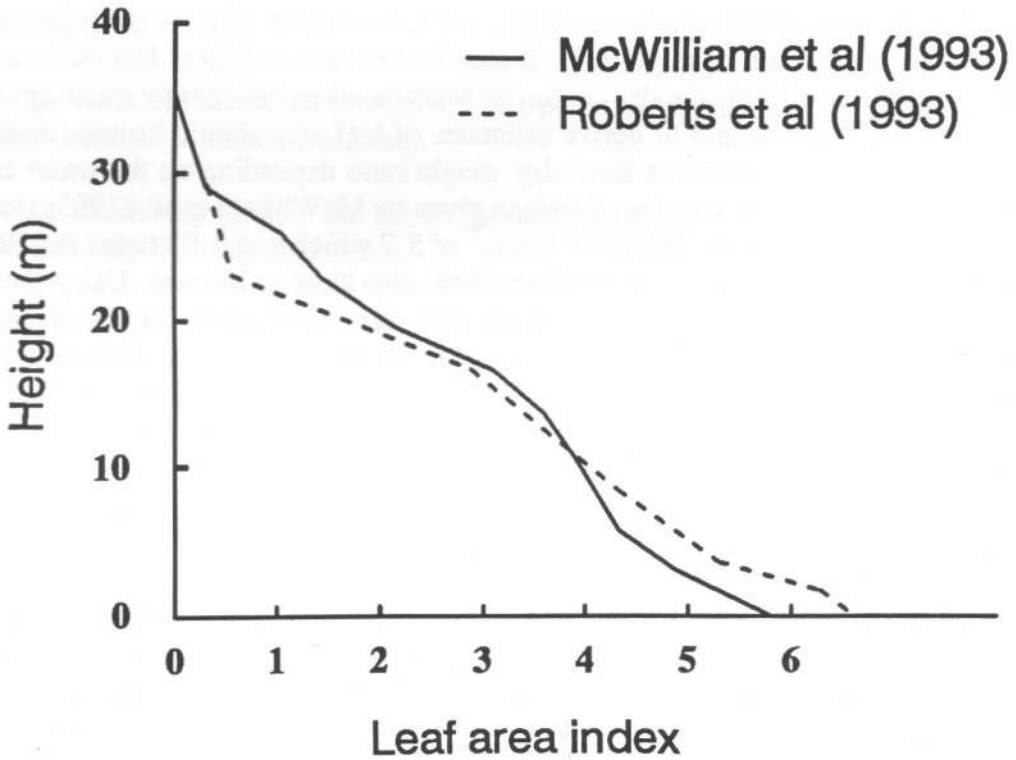


Figure 4. Cumulative leaf area index derived from literature values and used in CLATTER by Roberts et al., 1993 ( - - - ) and determined destructively by McWilliam et al., 1993 ( ——— ).



Site	Ji-Paraná	Manaus	Marabá
Method			
1). Litter area	4.63	6.1	5.38±0.43
2). Destructive sampling <sup>2</sup>	-	5.7±0.56	-
3). Literature	-	6.61 <sup>1</sup>	5.3 <sup>2</sup>
4). Optical method	4.4 <sup>3</sup>	-	-

1. Roberts et al., 1993, Klinge, 1973. Klinge et al., 1975.  
2. McWilliam et al., 1993. Higuchi et al., 1994.  
3. J. Grace (pers. comm. 1994).

**Table 3:** Leaf area index ( $L^*$ ) of ABRACOS forest sites.

Figure 5 shows specific leaf area,  $\delta_f$ , of living foliage taken from around the tower at Marabá and values obtained from the destructive sampling at Manaus by McWilliam et al., 1993. There is a decline in  $\delta_f$  from values between 4 and 6 at the tops of the canopies to values exceeding 12 at the canopy bases. Figure 6 shows that the bulk of litter falls into the same range of categories. The range of specific leaf areas for living leaves and the majority of litter leaves correspond to the range (8 - 27  $\text{m}^2 \text{kg}^{-1}$ ) which has been cited by Medina (1986) for studies in Malaysia and Central America and also shows that the frequency distribution of litter foliage over the range of  $\delta_f$  is very different and possibly offers a means of allocating the estimated total  $L^*$  to arbitrary canopy layers. Clearly the difference in  $\delta_f$  values from different canopy positions offers a way of identifying where and when litter of different canopy positions is falling. However Figure 7 shows the average monthly  $\delta_f$  for each sample taken throughout the two year period for which measurements were made at Marabá and shows that the mean litter  $\delta_f$  shows no consistent seasonal patterns implying that leaf fall is more or less equally distributed over the canopy each month.

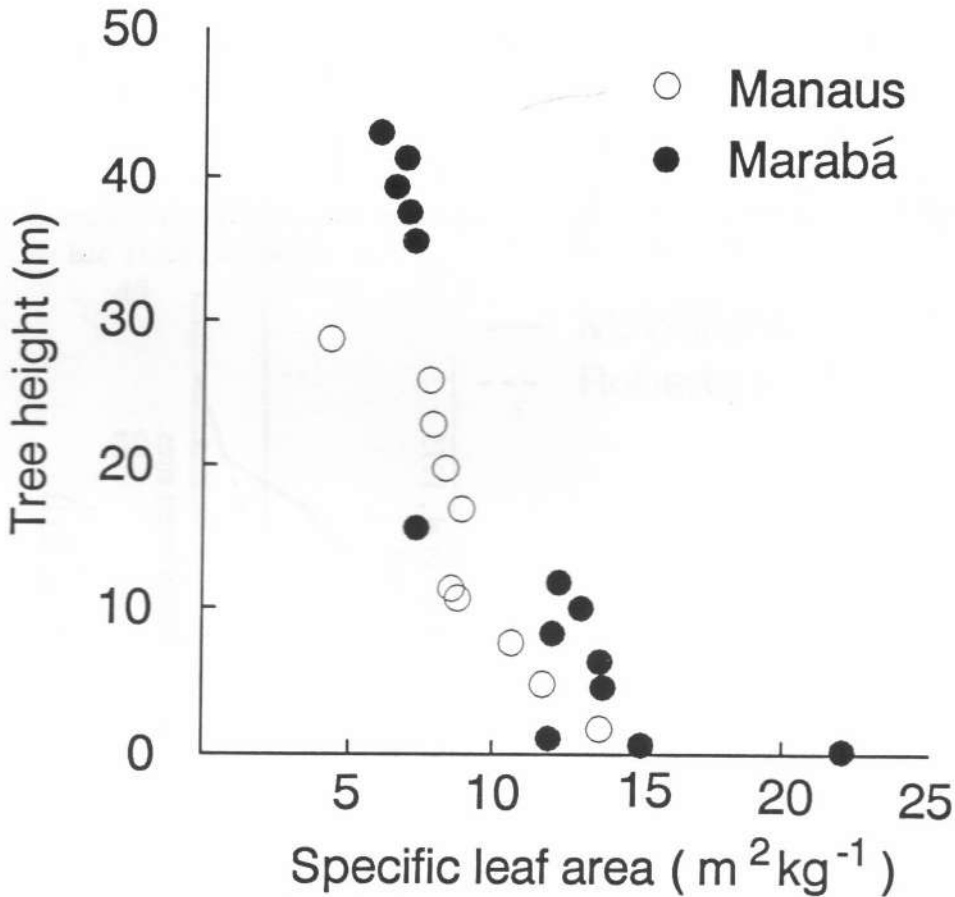


Figure 5. The relationship between specific leaf area (living leaves) with height in the canopy for the forests at Reserva Florestal Ducke, Manaus and Reserva Vale do Rio Doce, Marabá.

## Marabá - Specific Leaf Area Frequency Distribution

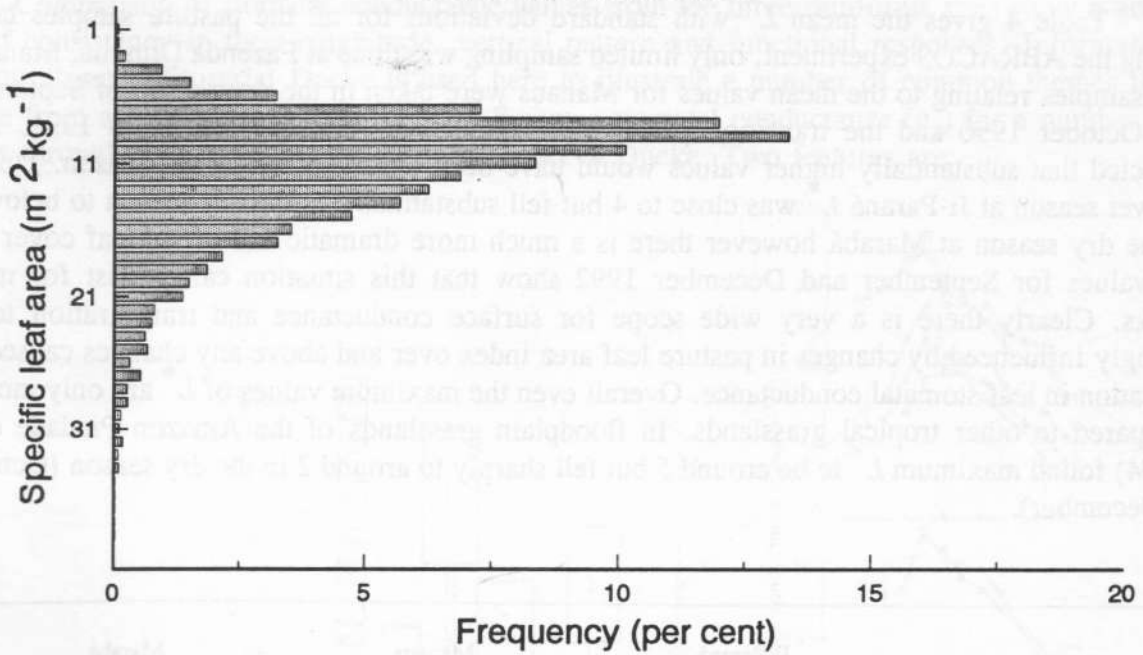


Figure 6. Frequency distribution of specific leaf area in the leaf litter fraction measured over 22 months at the Reserva Vale do Rio Doce, Marabá.

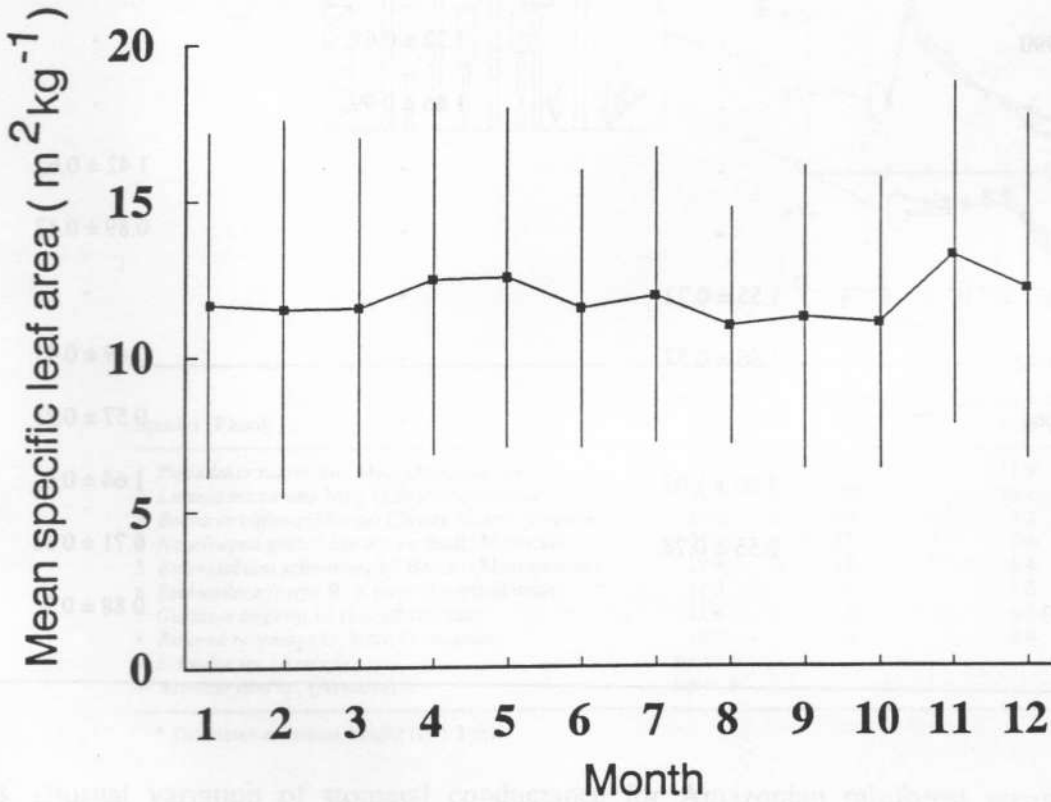


Figure 7. Monthly averages of specific leaf area from the Reserva Vale do Rio Doce, Marabá.

*Leaf area index - pasture*

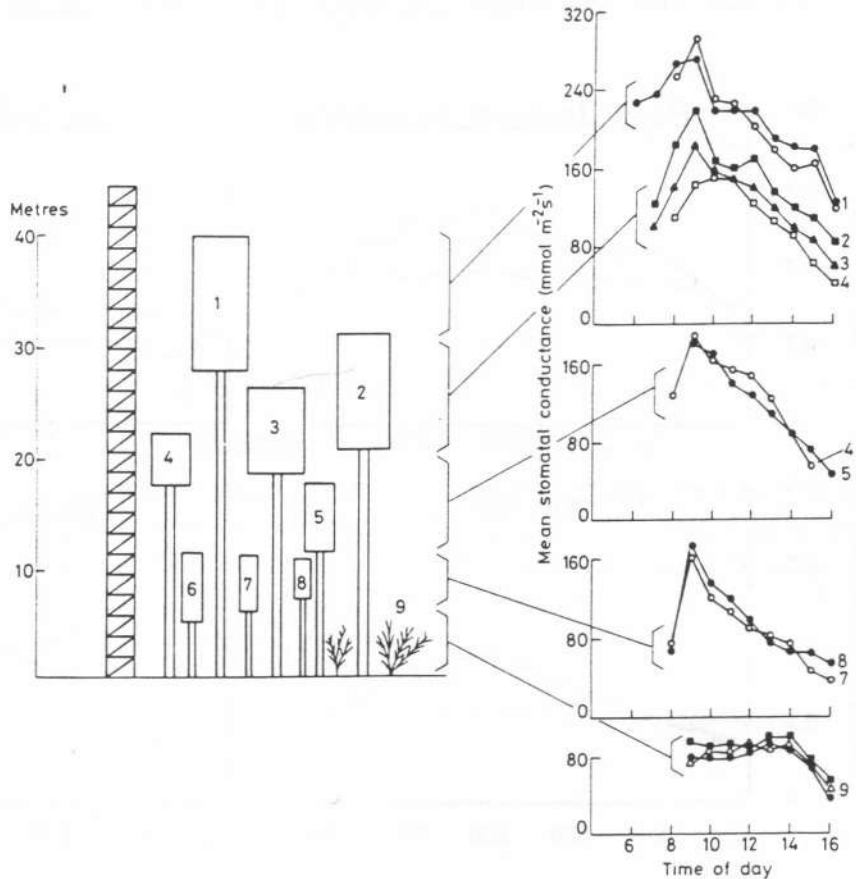
Table 4 gives the mean  $L^*$  with standard deviations for all the pasture samples taken during the ABRACOS experiment, only limited sampling was done at Fazenda Dimona, Manaus. The samples relating to the mean values for Manaus were taken in the dry season of September and October 1990 and the transition period between the wet and dry season in 1991. It is expected that substantially higher values would have been observed in the wet season. During the wet season at Ji-Paraná  $L^*$  was close to 4 but fell substantially in the dry season to below 2. In the dry season at Marabá however there is a much more dramatic fall off in leaf cover and the values for September and December 1992 show that this situation can persist for many weeks. Clearly there is a very wide scope for surface conductance and transpiration to be strongly influenced by changes in pasture leaf area index over and above any changes caused by alteration in leaf stomatal conductance. Overall even the maximum values of  $L^*$  are only modest compared to other tropical grasslands. In floodplain grasslands of the Amazon Piedade et al (1994) found maximum  $L^*$  to be around 5 but fell sharply to around 2 in the dry season (October to December).

Date	Ji-Paraná	Manaus	Marabá
September 1990	-	1.22 ± 0.61	-
July 1991	-	1.86 ± 0.99	-
January 1992	-	-	1.42 ± 0.62
June 1992	-	-	0.89 ± 0.47
August 1992	1.55 ± 0.72	-	-
September 1992	1.66 ± 0.57	-	0.49 ± 0.43
December 1992	-	-	0.57 ± 0.23
April 1993	3.90 ± 1.02	-	1.64 ± 0.6
June 1993	2.55 ± 0.78	-	0.71 ± 0.35
October 1993	-	-	0.88 ± 0.5

Table 4. Leaf area index ( $L^*$ ) of ABRACOS pasture sites

## Stomatal conductance - forest

Comparison of stomatal conductance values from the three rainforest sites show a good deal of consistency in their magnitude, vertical pattern and functional responses. Information from the Reserva Florestal Ducke is used here to illustrate a number of common themes that emerge from all three forest sites. Figure 8 shows stomatal conductance ( $g_s$ ) for a number of species throughout the height profile in the Reserva Ducke. Two features are



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		
<i>Astrocaryum</i> sp. (Araceae)	up to 3		

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

Figure 8. Diurnal variation of stomatal conductance for Amazonian rainforest measured at several levels within the canopy.



apparent which are common to the other two forest sites. The highest values occur at the top of the canopy and there is a systematic decline downwards through the canopy. The diurnal patterns are also consistent. At the top of the canopy, particularly, there is a sharp rise in  $g_s$  to the highest values which occur at mid morning and these then fall steadily throughout the day. This pattern becomes less pronounced lower in the canopy and at the canopy base  $g_s$  remains relatively constant throughout the day, only falling off at the end of the day. Figure 9 shows the response to above-canopy solar radiation on  $g_s$  of four species. There are some small seasonal differences but these may be related to leaf age rather than soil moisture effects.

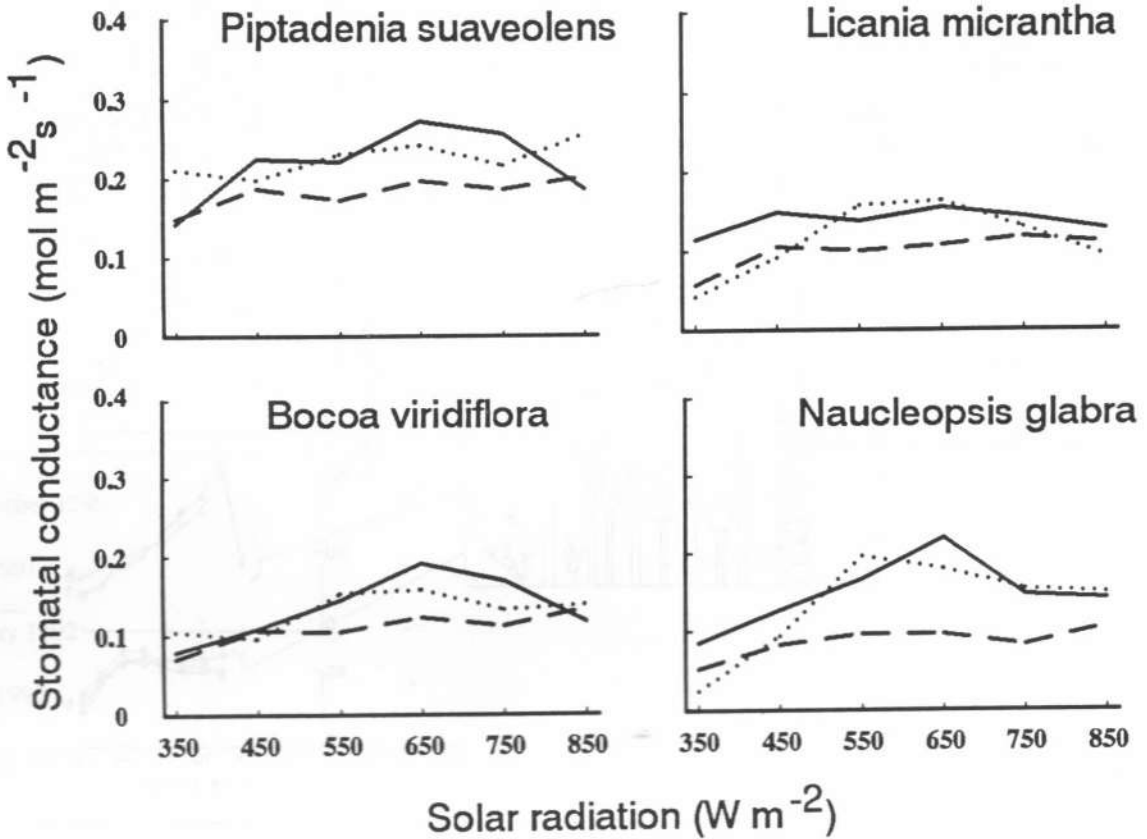


Figure 9. The relationship of stomatal conductance to above-canopy solar irradiance for four upper canopy species in three study periods, September 1983 (— — —), July-August 1984 (...) and March-April 1985 (————).

Figure 10 shows for *Piptadenia suaveolens*, an upper canopy species in the Reserva Florestal Ducke, the relationship between  $g_s$  and  $D$ . The significant negative relationships tend to show a declining slope with decreasing levels of radiation. Figure 11 shows a comparison of the responses of  $g_s$  of upper and lower canopy species to  $D$  and indicates consistent magnitudes and responses for the different sites for the same canopy levels.

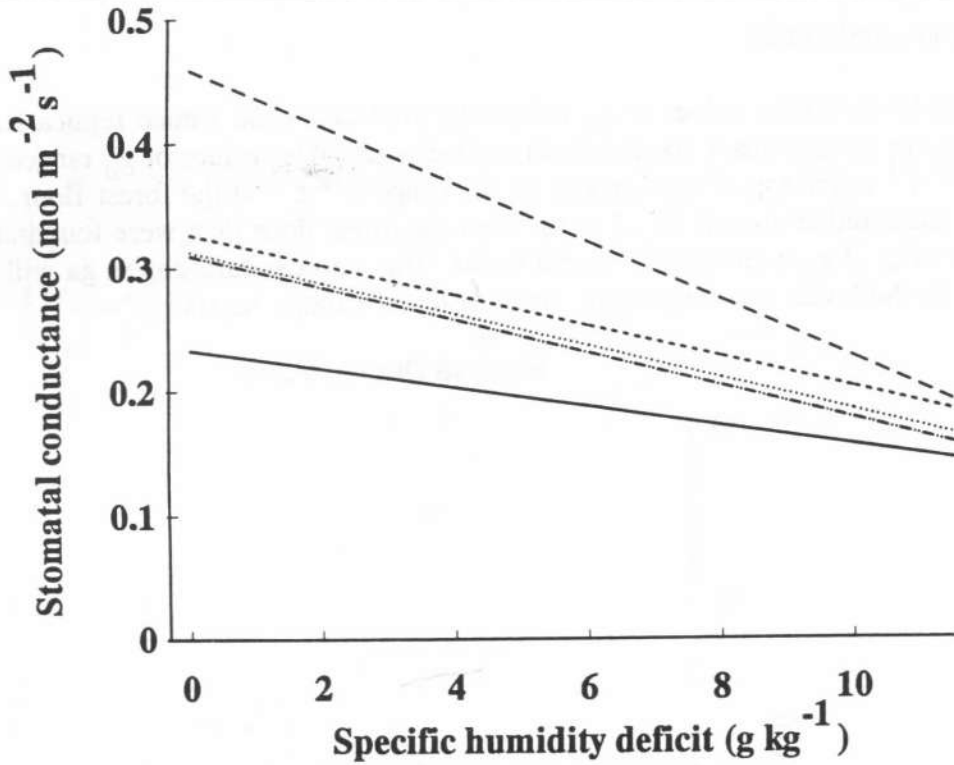


Figure 10. The relationship between stomatal conductance and specific humidity deficit for *Piptadenia suaveolens*, an emergent species, at the Reserva Florestal Ducke, Manaus. Data were pooled from three study periods but separated depending on above-canopy radiation  $< 400$  (————), 401-500 (-.-.-), 501-600 (.....), 601-700 (----) and 701-800 (— —)  $\text{W m}^{-2}$ .

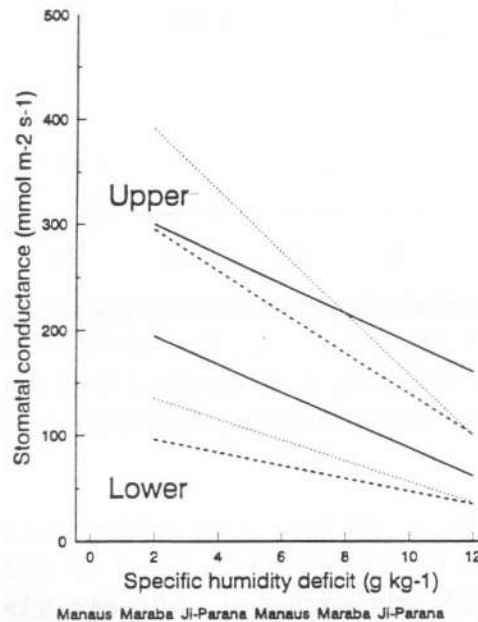


Figure 11. The relationship between stomatal conductance and air specific humidity deficit for an upper and a lower canopy species from each of the forests at Reserva Florestal Ducke, Manaus (————); Reserva Biologia Jaru, Ji-Paraná (.....) and Reserva Vale do Rio Doce, Marabá (- - -).

*Boundary layer conductance*

Figure 12 shows the values of  $g_a$  calculated from data from wetted replica leaves at ten levels through the canopy space for the Reserva Ducke site. The values of  $g_a$  ranged from over  $1.40 \text{ mol m}^{-2} \text{ s}^{-1}$  at the top of the canopy, to  $0.24 \text{ mol m}^{-2} \text{ s}^{-1}$  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 the relationship of  $g_a$  with height was not linear. This vertical variation in  $g_a$  will contribute substantially to the levels of transpiration from different canopy layers.

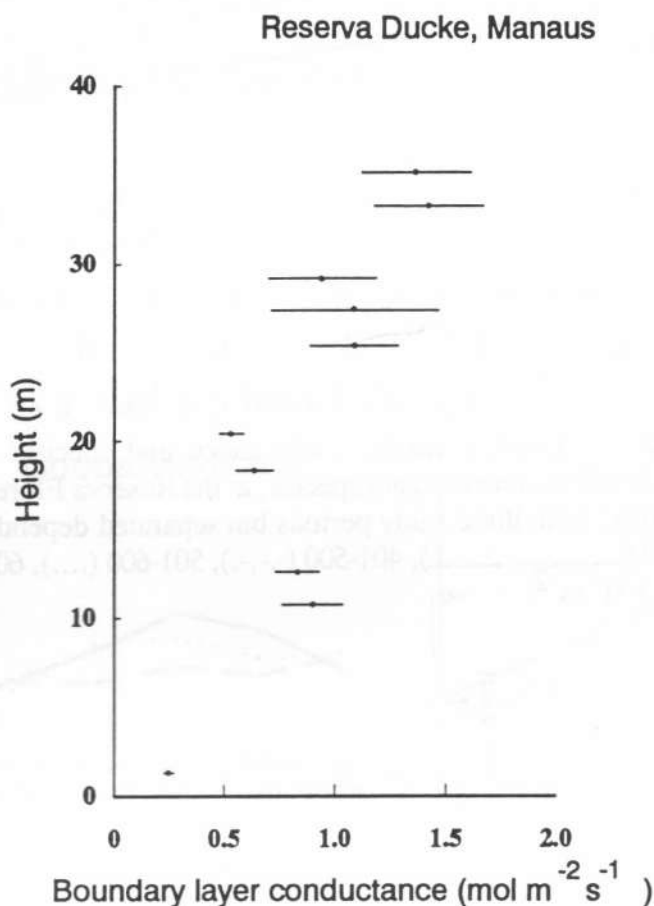


Figure 12. Variation of boundary-layer conductance with height in the forest canopy at the Reserva Florestal Ducke, Manaus, Amazonas. Horizontal bars indicate  $\pm 1$  sd.

*Within-canopy microclimate*

Figure 13 shows the hourly average of all the data taken during the daylight periods in July and August 1984 at different levels through and above the canopy. There is a slight depression in temperature and specific humidity deficit around 14h00 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 crowns of the emergent and subemergent trees probably

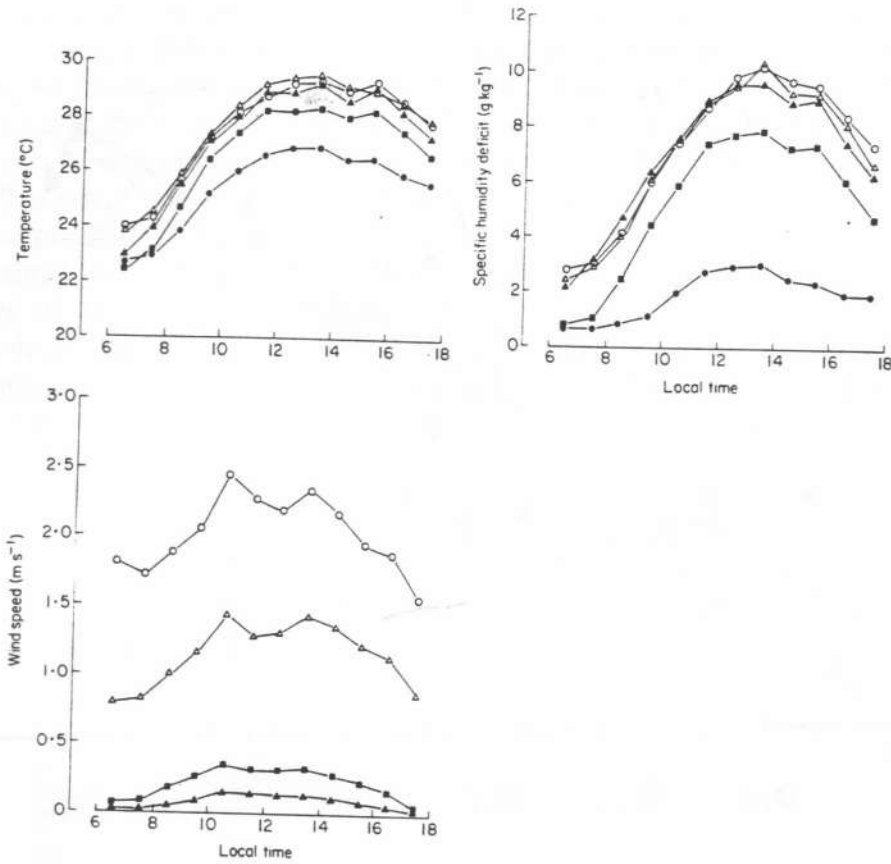


Figure 13. Hourly averages of temperature, specific humidity deficit and windspeed from measurements made in July-August 1984 at 1.45 m (●), 13.45 m (■), 23.25 m (▲), 35.69 m (Δ) and 44.66 m (○).

intercepted the major fraction of the above-canopy radiation above this level. Windspeed declines markedly through the canopy and at the lowest canopy measurement level anemometers were stalled almost permanently.

### *Rain forest transpiration*

CLATTER, the multi-layer canopy transpiration model has been implemented using data from the Reserva Florestal Ducke, Manaus as described above. The output from the model is compared with direct measurements of transpiration from an eddy correlation device, 'HYDRA'. Figure 14 shows the good correspondence of the hourly estimates from CLATTER compared with measurements from HYDRA, with the agreement being around 10 - 15 per cent. Table 5 shows the comparison of mean daily transpiration from CLATTER and HYDRA for four periods in different seasons.

## Reserva Ducke, Manaus

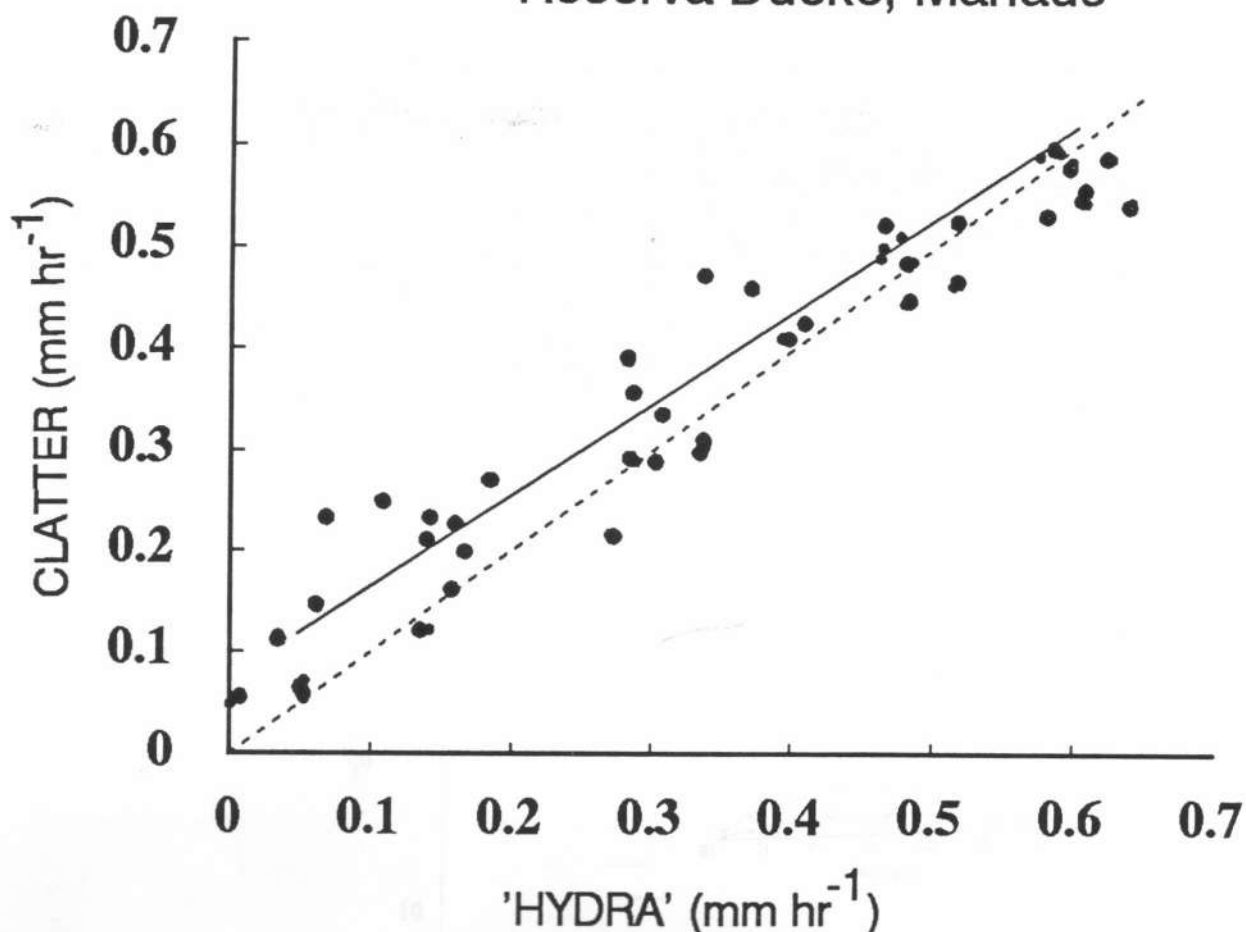


Figure 14. Estimates of hourly transpiration from the CLATTER model compared with measurements from the eddy correlation apparatus, 'HYDRA', the fitted regression is shown ( — ) as is the 1:1 relationship (....).

Period	'HYDRA'	CLATTER
September 1983	2.27	2.64
July/August 1984	4.55	4.54
April/May 1985	4.16	4.65
July/August 1985	3.71	3.77

Table 5. Mean daily transpiration rates ( $\text{mm day}^{-1}$ ) measured with an eddy correlation device ('HYDRA') compared with means of daily estimates from a transpiration model (CLATTER) for the same periods.



The CLATTER model also enables estimates to be made of the contribution of the different canopy layers to total forest transpiration and reveals the relatively greater role of upper canopy layers, where presumably most radiation interception takes place. Also of particular interest is the contribution which each canopy layer makes to the total transpiration compared to the percentage of the total  $L^*$  in each layer. Figure 15 reveals the different efficiency of upper and lower layers in contributing to the transpiration total. Currently many Global Climate Models have  $L^*$  of land cover implemented within them. Results of the type we have just shown imply that modification of this approach is necessary to take account of the different efficiency of different canopy layers. The lower efficiency of layers deeper in the forest canopy are a function of a number of factors: lower stomatal and boundary-layer conductances with the lower atmospheric demand conditions through lower net radiation and atmospheric humidity deficits. Although beyond the scope of this paper the CLATTER model also provides a useful tool to examine the consequences of manipulating forest structure on total transpiration and the relative contribution of different canopy layers.

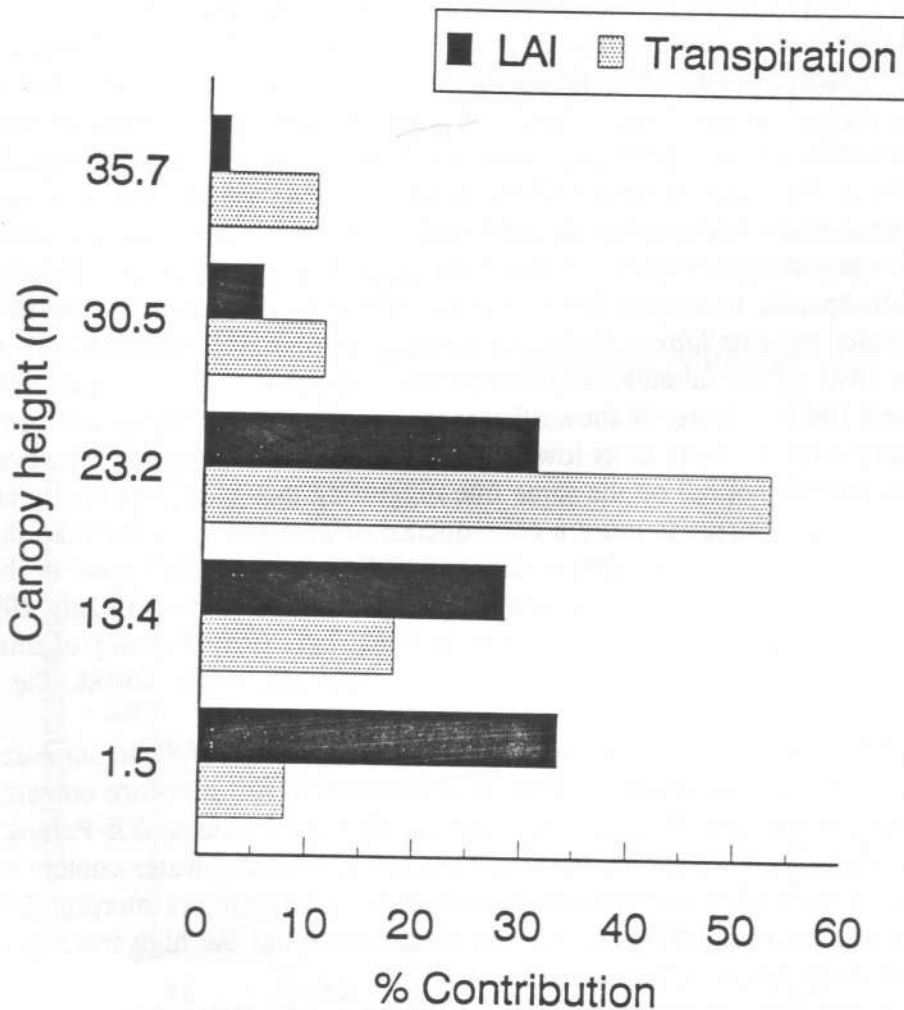


Figure 15. Percentage of total leaf area index and total transpiration calculated from the CLATTER model for the five layers of the forest canopy, Reserva Florestal Ducke, Manaus, Amazonas.

The CLATTER model has also been used successfully to estimate transpiration for Eucalyptus plantations in southern India (Roberts and Rosier 1993) and temperate broadleaf woodlands in England (Roberts and Rosier 1994). The understanding that has emerged from the CLATTER model for tropical forests so far is confined to the Reserva Ducke, Manaus. Future studies should implement physiological, canopy microclimate and canopy  $L^*$  data from the other ABRACOS forest sites to investigate in the same way, the relative importance of canopy layers and hence the effective  $L^*$ . At present it remains technically difficult to consider implementing a measurement programme for pastures which would emulate that made throughout the forest canopy and without these any approaches to scale pasture  $L^*$  with efficiency values in the same way as proposed here for forests would be premature.

### *Stomatal conductance - Pasture*

While there is consistency in the data for  $g_s$  from the three forest sites with respect to magnitude and responses for the pasture sites we see different responses particularly with respect to seasonal changes in soil water availability. At two of the sites, Fazenda Dimona, Manaus and Fazenda Nossa Senhora, Ji-Paraná  $g_s$  falls in response to declining soil water but this is not so clearly the case at Fazenda Boa Sorte, Marabá. Figure 16 shows the response of the two pasture species *Brachiaria humidicola* and *B. decumbens* to lowering of soil water storage between July and August 1991 at Fazenda Dimona. At the same time it is valuable to see the comparable values for woody shrubs which remain less affected by changes in soil water content presumably because of their deeper roots. Figure 17 shows the  $g_s$  of three shrub species almost double that of the *Brachiaria* species in August 1991. Figure 18 shows similar responses to lowering of available soil water by *Brachiaria brizantha* at the pasture site Fazenda Nossa Senhora, Ji-Paraná. In July 1993  $g_s$  has fallen to around half the value observed at the end of the previous wet season (April 1993). Figure 19 shows that there is a close relationship between  $g_s$  and  $\psi$  in both these seasons with  $\psi$  falling to as low as -2.0 MPa in the dry season. However the points from the two seasons do not fall on the same line suggesting that  $g_s$  is not directly controlled by  $\psi$  and that the leaf water status is more a consequence of changed  $g_s$  rather than the other way round. Leaf net photosynthesis ( $A$ ) data is also available from the IRGA used in the forest and pasture at Ji-Paraná. Figure 20 shows that with the drier soil conditions in July 1993  $A$  is less affected than  $g_s$  implying that under these circumstances water use efficiency of this  $C_4$  pasture species increases as soil water deficit increases. By contrast, in the forest, the relationship between  $g_s$  and  $A$  does not differ for different seasons.

Although maximum values are similar the behaviour of  $g_s$  of *Panicum maximum* at the Marabá pasture, Fazenda Boa Sorte in response to changes in soil moisture content is different from the *Brachiaria* species at the other two clearing sites at Manaus and Ji-Paraná. Figure 21 shows the maximum  $g_s$  values for *P. maximum* plotted against soil water content and indicates the highest conductances when soil moisture is least. This relationship is interpreted by regarding soil moisture as having very little influence on conductance but the high irradiance associated with dry periods does influence the level of  $g_s$ .

Figure 22 shows that there also seems to be a link between  $g_s$  and atmospheric humidity deficit in *P. maximum* at Marabá which is not evident in the *Brachiaria* species at the other two pasture sites.

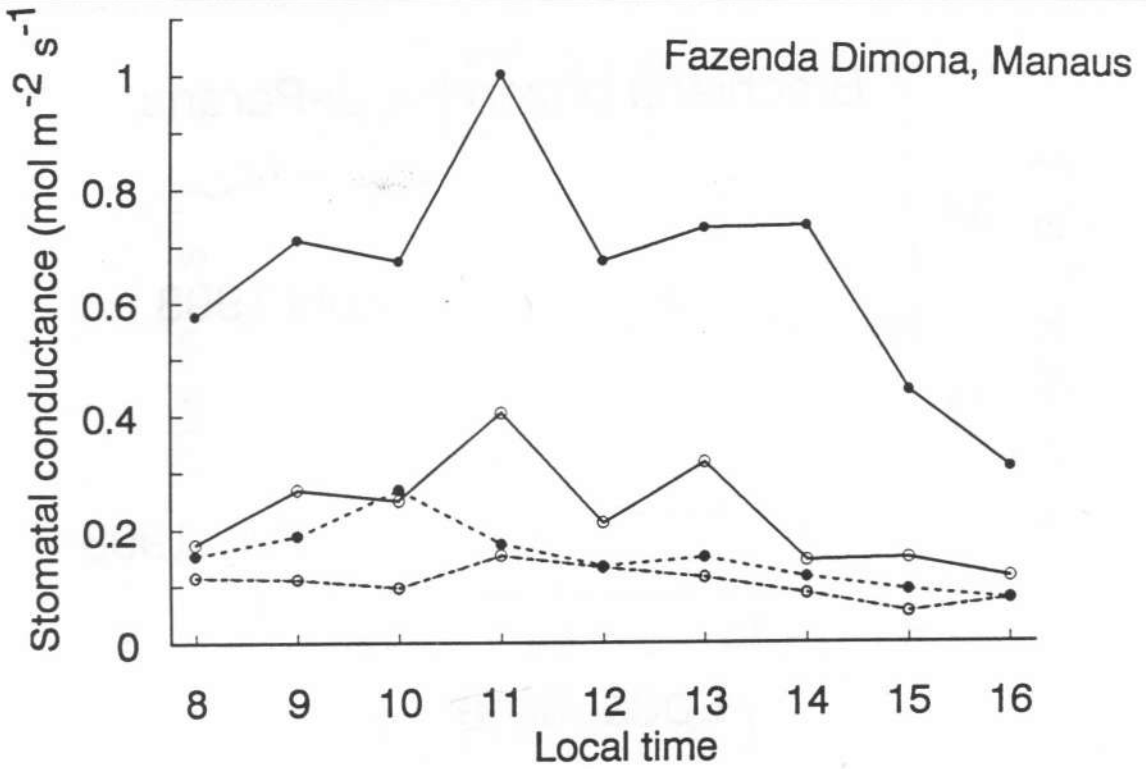


Figure 16. Diurnal averages of stomatal conductance for *Brachiaria decumbens* (●) and *B. humidicola* (○) in July (—) and August (---) 1991 in pasture at Fazenda Dimona, Manaus.

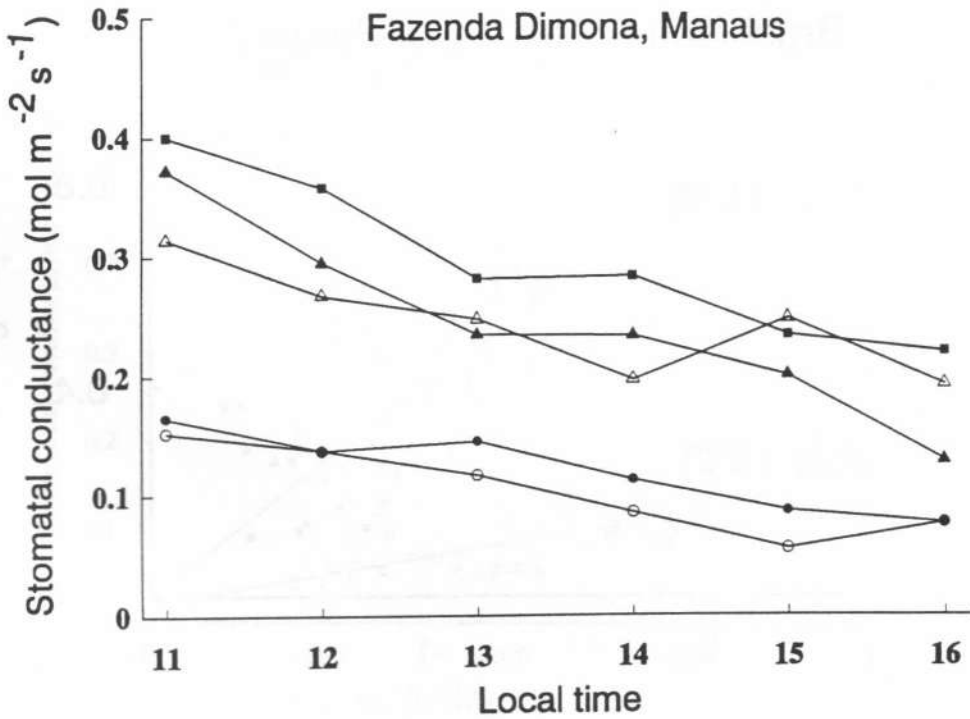


Figure 17. Diurnal changes in stomatal conductance of three shrub species (■,▲,△) and *Brachiaria decumbens* (●) and *B. humidicola* (○) in the pasture at Fazenda Dimona, Manaus.

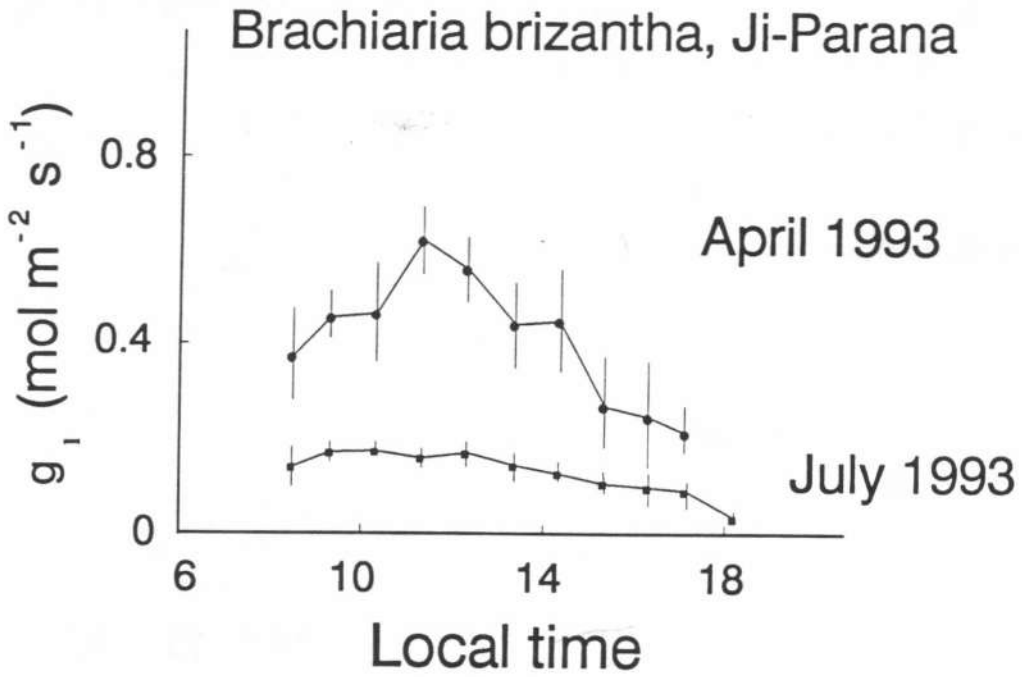


Figure 18. Diurnal changes in stomatal conductance of *Brachiaria brizantha* at Fazenda Nossa Senhora, Ji-Paraná, Rondonia. Data from the end of the wet season, April 1993 and in the dry season, July 1993.

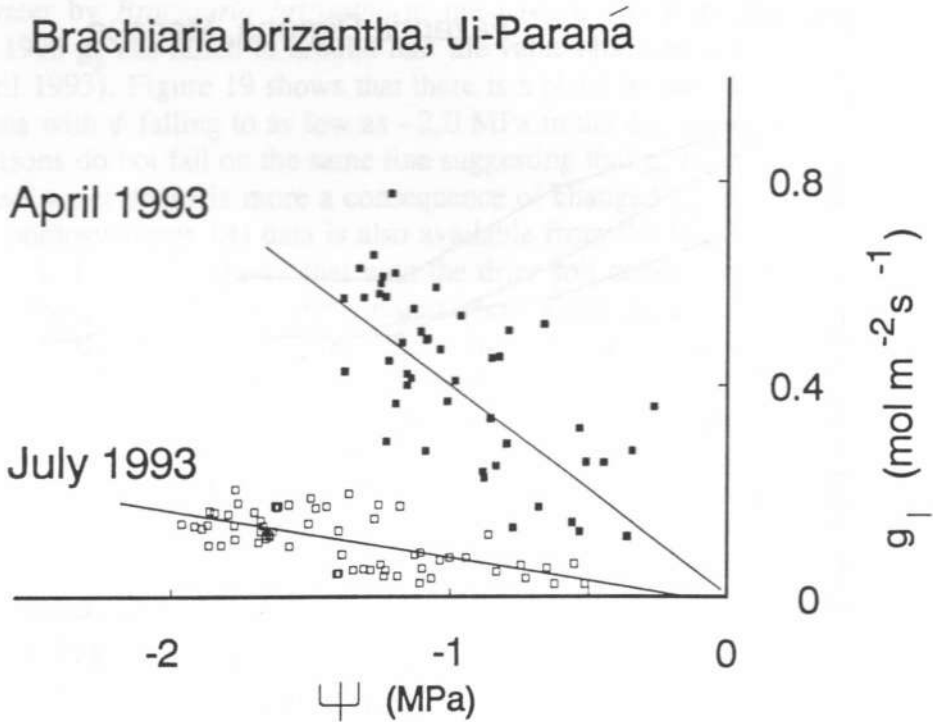


Figure 19. The relationship between stomatal conductance and leaf water potential of *Brachiaria brizantha* at Fazenda Nossa Senhora, Ji-Paraná, Rondonia. Data from the end of the wet season, April 1993 and in the dry season, July 1993.

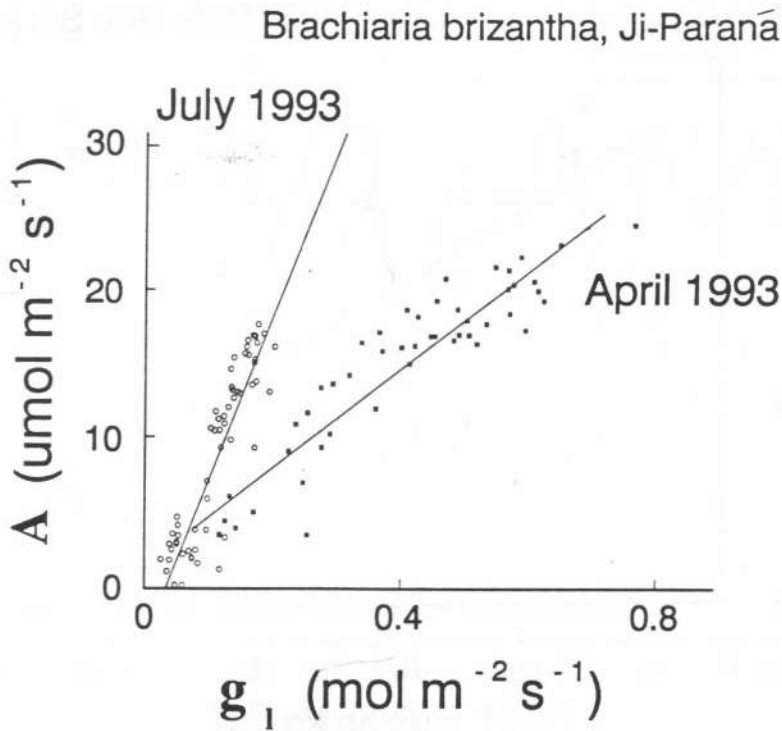


Figure 20. The relationship between leaf stomatal conductance and leaf net photosynthesis of *Brachiaria brizantha* at Fazenda Nossa Senhora, Ji-Paraná, Rondonia. Data from the end of the wet season, April 1993 and in the dry season, July 1993.

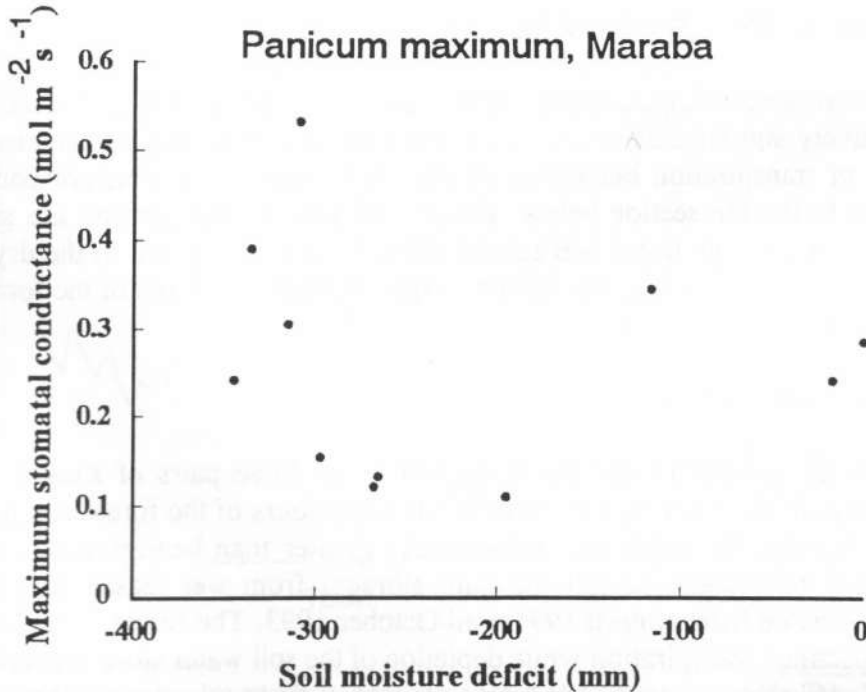


Figure 21. Maximum stomatal conductance of *Panicum maximum* plotted against associated soil moisture deficit in eleven measurement missions at Fazenda Boa Sorte, Marabá, Pará.



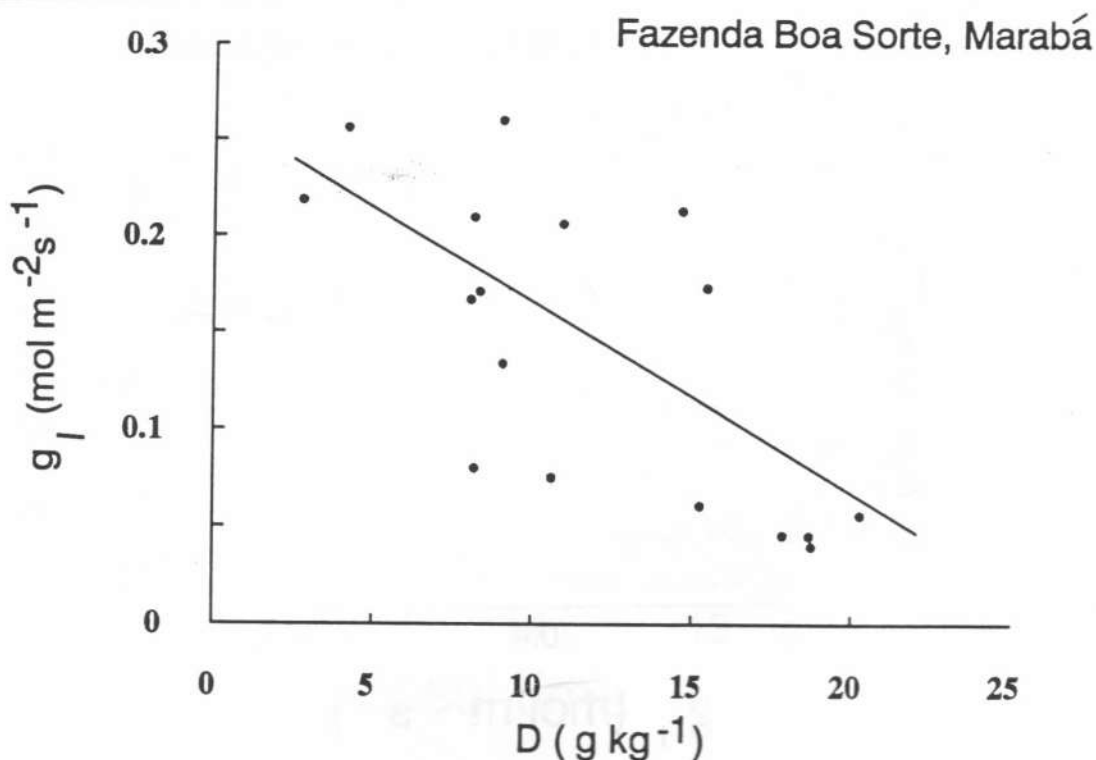


Figure 22. Relationship between average  $g_s$  of *Panicum maximum* between 1000 and 1400 hours in the pasture at Fazenda Boa Sorte, Marabá and associated air specific humidity deficit.

#### *Micrometeorological studies - Forest and pasture*

Detailed micrometeorological comparisons have only been made at Ji-Paraná and Manaus and show qualitatively similar behaviour. The results are also in complete agreement with the different patterns of transpiration behaviour which emerge from soil moisture content studies which are referred to the the section below. Forest and pasture transpiration are similar when soil moisture contents are high in the wet season and the transition period to the dry season but as Figure 23 shows pasture transpiration falling to approximately half that of the forest after less than two weeks without rain.

#### *Soil moisture abstraction - Forest and pasture*

The studies of changes in soil water content at the three pairs of sites in ABRACOS showed qualitatively similar patterns for the different behaviours of the forest and pasture. Soil water abstraction beneath the forest was substantially greater than beneath pasture. Figure 24 shows a comparison of changes in soil moisture storage, from wet season saturated values, beneath forest and pasture from August 1991 until October 1993. The forest maintains soil water abstraction with sustained transpiration while depletion of the soil water store beneath the pasture declines after periods in the wet season and the transition period to the dry season at which time rates are equal to those of the forest. A very interesting and important result emerging from the Marabá forest results (Figure 24) is the pattern at the end of 1992 when there was insufficient rainfall to replenish the soil water store. At the beginning of the

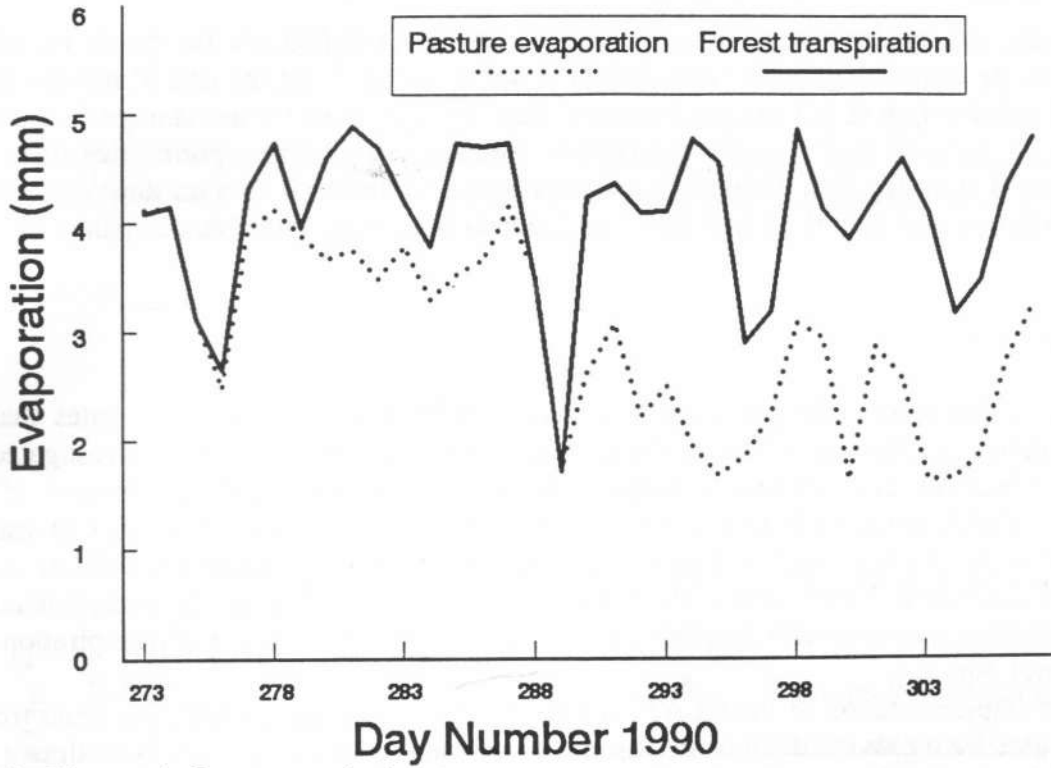


Figure 23. Changes in forest transpiration (————) and pasture evaporation (.....) over a rainless period in October 1990.

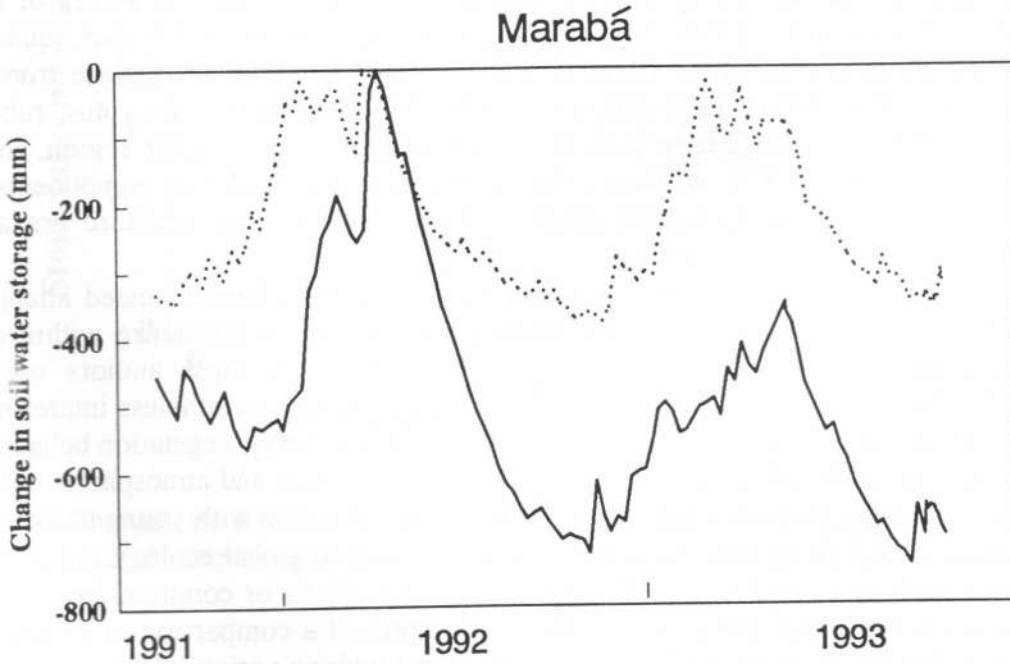


Figure 24. Changes in soil water storage beneath forest at Reserva Vale do Rio Doce, Marabá (————) and pasture at Fazenda Boa Sorte, Marabá (.....).

following dry season there was still a substantial soil water deficit but the forest maintained transpiration by abstracting water from deeper layers in the soil. At the end of the dry season the rate of transpiration of the pasture estimated from changes in soil water storage fell to levels as little as 25 per cent of that in the wet season. Hodnett et al (1995) reported that these rates were around  $1 \text{ mm day}^{-1}$  at Fazenda Nossa Senhora, Ji-Paraná,  $0.75 \text{ mm day}^{-1}$  at Fazenda Dimona, Manaus and only  $0.61 \text{ mm day}^{-1}$  at Fazenda Boa Sorte, Marabá.

## Discussion

No evidence has emerged from our studies at three tropical rainforest sites that soil moisture deficit influences stomatal conductance. Nepstad et al. (1994) investigated the relationship between evergreenness in tropical forest in the Amazon and the presence of deep roots. The authors found roots to about 10 metres in the central Amazon even though seasonal soil moisture deficits are small. Using a simple soil water balance model and rainfall records from the Manaus area Hodnett et al. (1995) showed that in 7 out of the past 27 years low rainfall would probably have meant that deep rooting would have a role in sustaining transpiration even in the central Amazon.

The implementation of the CLATTER model for estimating transpiration from tropical rainforest used field data but there is no reason why information could not equally be drawn from published literature although up to now this approach has been limited by the lack of completeness of datasets from any one locality and only studies in ARME and ABRACOS have provided such complete data. The approach of implementing literature derived values of leaf conductance and leaf area with microclimate data into a form of the Monteith-Penman equation is an attractive alternative to direct field measurement for crops which might replace tropical forest. Sufficient information should be available for crops such as oil palm, eucalyptus, rubber and coffee but for other crops, especially perhaps fruits endemic to the Amazon region, there seems to be very limited data. Many of these crops might also be involved as components in agroforestry systems and estimation models adapted to that type of crop structure are also available (Shuttleworth and Wallace, 1985).

Korner (1994), Schulze et al. (1994) and Kelliher et al. (1995) have focussed attention on the consistency of the values of maximum stomatal and surface conductance within and between major vegetation types. Although the statistical limits that these authors use to encompass data regarded as similar is rather large the observations are nevertheless interesting. However, maximum conductances are only of limited value for describing vegetation behaviour because they are derived from limited periods of the day when radiation and atmospheric deficit are optimal and in particular seasons when soil water levels are adequate with young unstressed leaves. Schulze et al (1994) claim their summary is a contribution to global ecology but it must be a limited one as ecology is concerned with responses of individuals or communities to their environment and presumably changes in it. An important aspect of a comparison of maximum conductances which has not received sufficient attention is that under a variety of circumstances plants with the highest conductances are those which show the greatest change in value in response to some stress factor. We have seen this here in own data where high leaf conductances in the upper canopy or in high radiation fall off more sharply. There however good examples from the literature. Figure 25 shows a similar effect in the range of stomatal conductances for a number of temperate tree species Data from Federer (1977). Figure 26 shows transpiration measured against soil water availability in a number of studies collated by Rutter (1968). The forest with high transpiration were limited more early on than those forests which transpired more moderately. Figure 27 comes from the classic work of Denmead and Shaw (1962) and

shows a similar type of response with wheat. Clearly then we need to be somewhat cautious about using maximum stomatal conductance to categorize vegetation when some of the compensating mechanisms we have shown are operating. Furthermore Korner (1994) believes that in practice generally that maximum  $g_s$  rarely falls below 10 per cent of the maximum but it is difficult to reconcile this view with the data we have observed in Brazil and other substantial amounts of evidence already published.

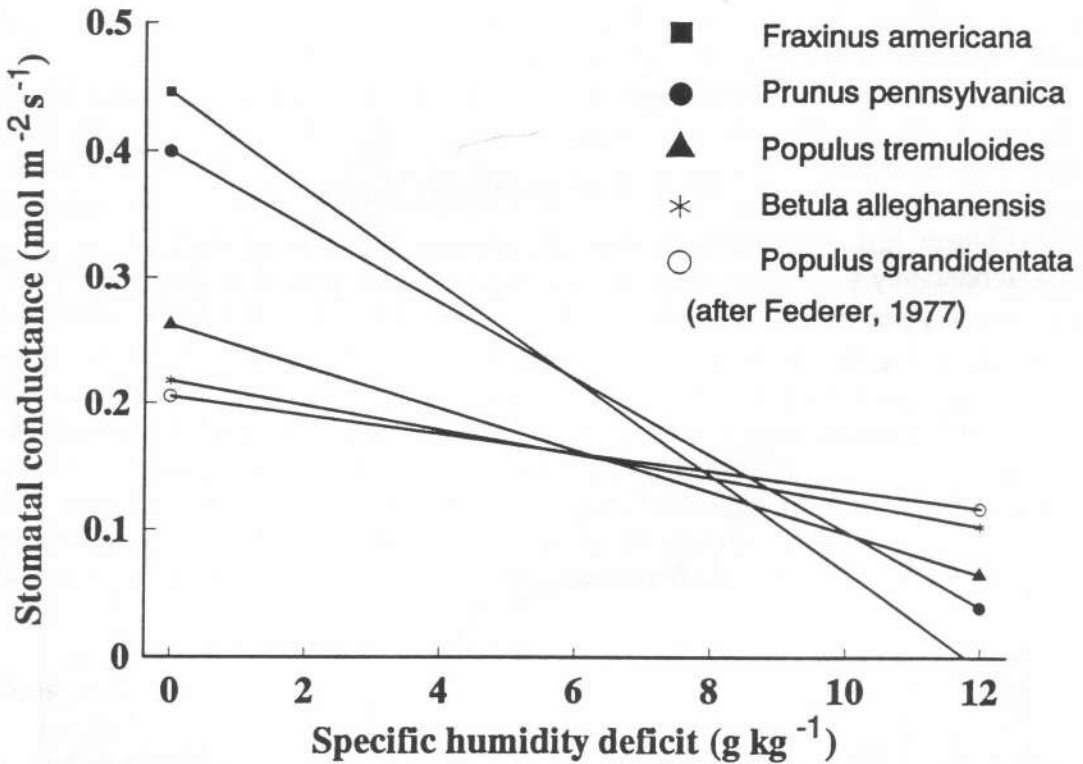


Figure 25. Changes in stomatal conductance with increasing atmospheric humidity deficit in several temperate broadleaf species. Data redrawn after Federer (1977).

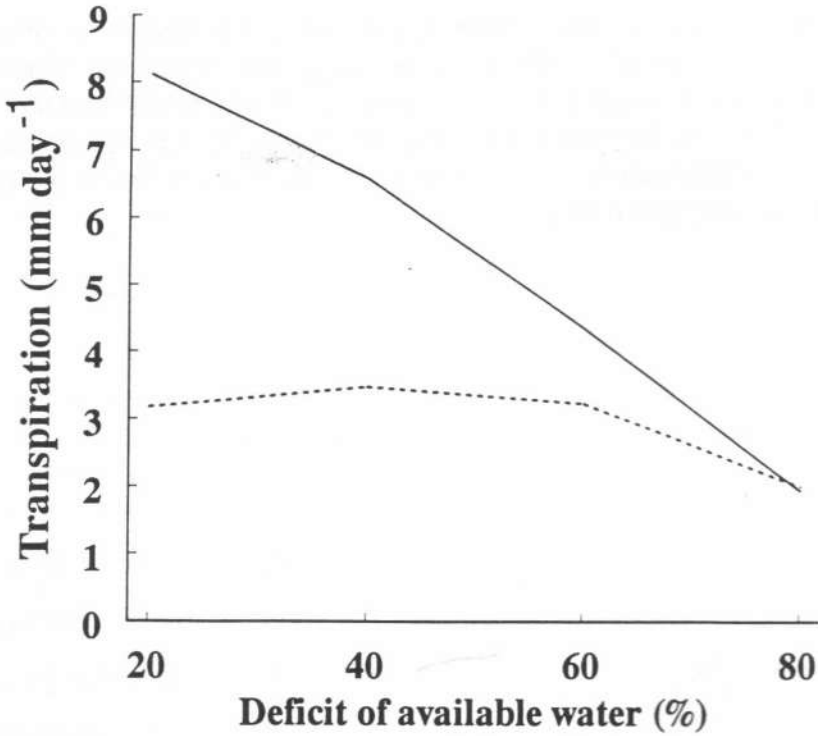


Figure 26. Changes in daily transpiration with deficit of available water for rapidly (—) and moderately (- -) transpiring forests. Data redrawn after Rutter (1968).

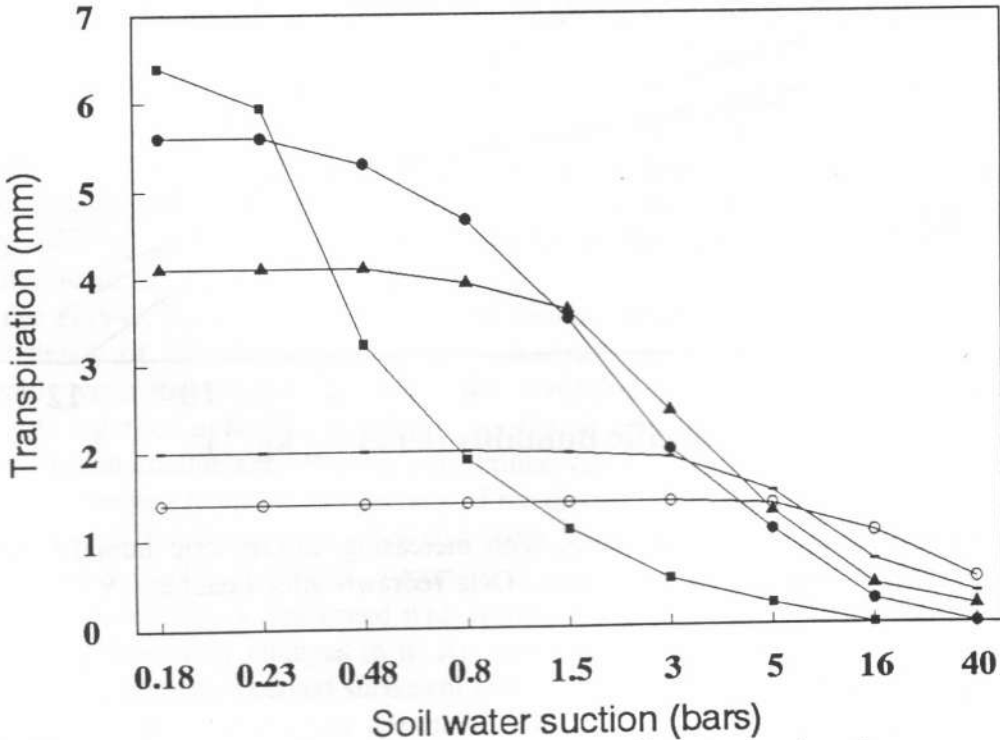


Figure 27. Changes in transpiration rate in response to soil water suction for a range of initial rates at field capacity, data after Denmead and Shaw, 1962).

There is however a great deal of published values for many tropical forest trees and many of these have been collated in Table 6. Mostly the values fall into a broad range but some very high values have been reported. The values published by Whitehead et al (1981) and Grace et al (1982) for *Tectona* and *Gmelina* are especially high. Most leaf photosynthesis values reported for tropical forest trees are quite moderate. Only a limited of studies of leaf water potential have been made and it is notable that values as high as 4.0 MPa can be sustained at the top of some of the rainforest in Brazil. Although some types of tropical rain forest have been relatively well studied although Bruijnzeel and Proctor (1995) extensively reviewed hydrological and biogeochemical data from Tropical Cloud Montane Forests and drew attention to the very limited amount of physiological data for this vegetation type. Paradoxically it seems that there should be more effort put to physiological studies of tropical pasture species, secondary forests, tropical forests and agroforestry systems.

Many published studies in Table 6 can be used to illustrate a negative correlation between  $g_s$  atmospheric humidity deficit. This link is very relevant to modelling stomatal behaviour and this negative correlation is strongly involved in maintaining transpiration at moderate levels in rainforest. Monteith (1995 a and b) has reappraised the correlative links between stomatal conductance and saturation vapour pressure deficit of the atmosphere and concludes that many of these correlations are stronger between stomatal conductance and transpiration rate. Monteith makes this point well graphically and rightly points out that up to now the evidence for a sensor for humidity in plant leaves which could be linked to stomata closure has yet to be shown unequivocally. Nevertheless, there still remains considerable value in the strong correlations shown between  $D$  and  $g_s$  because in a wide number of cases these two parameters are measured but transpiration is not. This will certainly be the case when the principal or sole measurement is stomatal conductance is determined by porometry not from transpiration by inverting the Penman-Monteith equation. Although some technical advances have been made to stem heat balance and heat pulse velocity techniques to measure transpiration they are not sufficiently advanced to accommodate emergent, main canopy or even subcanopy trees in tropical rainforests. Therefore approaches to estimate leaf transpiration or canopy layer transpiration in such circumstances will still largely rely on porometer measurements.

## Conclusions

1. Future studies should incorporate more detailed phenological studies which would enable leaf physiology to be better linked to leaf age. Details of average leaf life span are also required to enable exact values for leaf area index to be determined.
2. More information is required on rooting depths and therefore the "effective" soil water store which may determine the response of tropical rainforest to infrequent dry conditions occurring naturally or the likely response of forest to a climate shift resulting in drier conditions.

**Table 6.:** Published values of stomatal conductance ( $g_s$ ), net photosynthesis ( $A$ ) and leaf water potential ( $\psi$ ) with authors.

Country/Species	$g_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	$A$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	$\psi$ (MPa)	Reference
<b>AUSTRALIA</b>				
<i>Agroderdron paraltum</i>	0.170	9.4	-	Pearcy (1987)
<b>BRAZIL</b>				
<i>Piptadenia suaveolens</i>	0.290	-	-3.80	Roberts et al (1990)
<i>Licania micrantha</i>	0.220	-	-	"
<i>Bocoa viridiflora</i>	0.185	-	-2.60	"
<i>Naucleopsis glabra</i>	0.160	-	-	"
<i>Cedrella odorata</i>	0.552	12.6	-2.64	McWilliam et al (1995)
<i>Inga spp.</i>	0.556	12.9	-2.41	"
<i>Bertholettia excelsa</i>	0.400	-	-3.5	Sá et al (1995)
<b>CAMEROON</b>				
<i>Sacoglottis gabonensis</i>	0.320	11.0	-	Koch et al (1994)
<i>Dialium pachyphyllum</i>	0.32	10.0	-	"
<b>COSTA RICA</b>				
<i>Goethalsia meiantha</i>	-	6.5	-	Stephens & Waggoner (1970)
<i>Pentaclethra macroloba</i>	0.160	-	-	Oberbauer et al (1987)
<b>JAMAICA</b>				
<i>Clethra occidentalis</i>	0.280	-	-	Aylett (1985)
<i>Cyrilla racemosa</i>	0.300	-	-	"
<i>Hedyosmum arborescens</i>	0.104	-	-	"
<b>MALAYSIA</b>				
various species	-	12.6-18.9	-	Koyama (1981)



CONTINUED

<b>MEXICO</b>					
<i>Jacquinia pungens</i>	0.188	-	-		Fanjul & Barradas (1985)
<i>Coccoloba liebmanni</i>	0.236	-	-		"
<i>Piper auritum</i>	0.700	-	-		Chiarello (1984)
<i>Piper hispidum</i>	1.000	-	-		Mooney et al (1984)
<b>NIGERIA</b>					
<u>Wet season</u>					
<i>Tectona grandis</i>	1.2	-	-1.0		Grace et al (1982)
<i>Gmelina arborea</i>	1.0	-	-1.0		"
<u>Dry season</u>					
<i>Tectona grandis</i>	1.2	-	-1.2		Whitehead et al (1981)
<i>Gmelina arborea</i>	0.6	-	-2.0		"
<b>PANAMA</b>					
<i>Anacardium excelsum</i>	0.300	-	-		Meinzer et al (1993)
<i>Trichilia cipo</i>	0.390	-	-		Fetcher (1979)
<i>Cordia alliodora</i>	0.260	-	-		"
<b>THAILAND</b>					
<i>Hopea ferrea</i>	0.420	-	-		Pitman (unpublished)
<b>VENEZUELA</b>					
<i>Podocarpus rospigliossi</i>	0.135	-	-		Meinzer et al (1984)
<i>oleifolius</i>	0.155	-	-		"

3. There is a scarcity of information about the physiological responses of trees invading treefall gaps. Most information in the literature relates to mature trees under stable conditions. This type of information is also scarce for secondary forests. This type of information might then be relevant to understanding the key role that regenerating secondary forests may have as the fallow vegetation in "slash and burn" agriculture.
4. In the case of both ARME and ABRACOS studies have been confined to plateau sites within the topographically heterogeneous landscapes of Amazonia. We need to extend our studies to slope and valley bottom sites whose seasonal water supply will differ and may also be floristically different.
5. The magnitude and response of  $g_s$  of shrubs invading Amazonian pastures differ from the pasture in drying conditions and probably relates to deeper rooting of the shrubs. There is uncertainty about the period before abandoned pasture resumes the functional behaviour of rainforest.

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