Transpiration from an Amazonian rainforest calculated from stomatal conductance measurements

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Abstract

A multi-layer combination equation has been used to calculate transpiration from a tropical rainforest in the central Amazon, Brazil The five-layer formulation used through-canopy measurements of temperature and humidity deficit with leaf stomatal and boundary layer conductances scaled up to canopy layer values used a profile of canopy leaf area index derived from the literature Net radiation input to each layer was estimated from an above canopy measurement using an extinction function and leaf area index

Transpiration calculated for hourly and daily periods in a range of seasonal conditions agreed well with those measured directly with an eddy correlation device Four simplified forms of the transpiration calculation were also compared with the direct measurement These simplified forms used the above-canopy or the average of the through-canopy values of weather variables and used either the average of leaf conductances multiplied by total leaf area index or the average of the layer conductances These simplified forms of the transpiration calculation gave poorer agreement with measured transpiration

Introduction

Complete or partial clearance of tropical rainforest affects large-scale surface energy balance and carbon dioxide content of the atmosphere, as well as local streamflow and soil stability The consequences of changes in the extent of tropical forests have been difficult to assess because of a shortage of information and understanding of the water, carbon and nutrient cycles of different forest types (Mooney et al , 1980)

In the last decade, however, there has been a substantial increase in the number of physiological studies of rainforest species, some of which have included detailed studies of leaf gas exchange and associated weather vari-

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ables throughout the height profile of the forest canopy (e g Oberbauer et al , 1987, Roberts et al , 1990) The data derived in such studies have at least a two-fold value Firstly, direct studies of stomatal behaviour, leaf gas exchange and their interaction with weather variables and soil water status can aid interpretation and modelling of water and CO_2 fluxes determined micrometeorologically, and in this way aid the realism of hydrological and Global Climate modelling exercises (e g Shuttleworth, 1988, Sellers et al , 1989) Secondly, the physiological data on stomatal and boundary-layer conductances and leaf area index can be used to provide a direct estimate of transpiration from rainforest canopies

As micrometeorological measurement of transpiration fluxes from vegetation can be expensive and time-consuming for tall forest canopies, there is merit in evaluating the scope for exploiting existing physiological data for tropical rainforests to estimate transpiration using combination formulae in which these physiological data can be used in association with measured weather variables Although such combination formulae (e g Monteith, 1965) are now widely used for crops and other simple vegetation covers, their applicability to complex tropical rainforest canopies remains untested

The objectives of the studies presented here are three-fold, namely (1) to evaluate a multi-layer version of the Monteith–Penman formula which incorporates physiological and micrometeorological data taken at a primary rainforest site in the central Amazon against direct measurements of transpiration made at the same site, (ii) to determine the relative importance of different input variables for such an equation, (iii) to assess the validity of simplifying this multilayer approach towards combination formulae of increasing simplicity

Materials and methods

Site

The experimental site was in terra firme forest in the Reserva Florestal Ducke, 25 km from Manaus, Amazonas, Brazil ($2^\circ 57'$S, $59^\circ 57'$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 forest canopy

A 44 m high sectional aluminium tower was installed in the forest on which micrometeorological equipment were mounted through and above the forest canopy (Shuttleworth et al , 1984a, b) Plant physiological measurements were made on foliage accessible from the tower, and on shorter vegetation at ground level within 100 m of the tower (Roberts et al , 1990)

Microclimate

The microclimate measurements used in the present study were above-

canopy solar and net radiation, and the dry and wet bulb temperatures of the air measured with fully ventilated and shielded quartz-crystal psychrometers of the type described by Gash and Stewart (1975) The data used comes from a psychrometer mounted above the canopy at 44 m, and others at 35 7, 30 5, 23 2, 13 5 and 1 4 m above the forest floor within the forest Hourly average values were used in all the following analyses

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

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

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*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, δq_i is canopy layer specific humidity deficit, Δ'_i is the rate of change of saturated specific humidity with Δ'_i temperature at the canopy layer, λ is latent heat of vaporisation of water and ρ 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*th layer in the forest canopy is approximated by the Beer–Lambert Law

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

where $R_{n,i}$ is the radiation beneath the *i*th canopy layer, $R_{n,o}$ is the net radiation above the canopy, *k* is an extinction coefficient (taken here as 0 6), L_j^* is the leaf area index of layer *j* (where *j* = 1 to *i*)

This value of *k* combined with the L^* estimated a residual net radiation at the forest floor of 2 5% 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

$$g_{c\,i} = L_i^* g_{s\,i} \tag{3}$$

where L_i^* is the leaf area index of a given canopy layer and $g_{s\,i}$ is the leaf stomatal conductance a given canopy layer

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

Stomatal conductance

Roberts et al (1990) describe results from a detailed investigation of stomatal conductance (g_s) for rainforest canopy at the Reserva Ducke site used in this study These results encompassed the diurnal variation encountered throughout the forest canopy, and were collected in three measurement periods coinciding with different seasons in 1983, 1984 and 1985 Differences in g_s between seasons were observed to be small, but there was a substantial variation associated with position in the canopy, and large diurnal trends which are correlated with diurnal changes in solar radiation and atmospheric humidity deficit

Roberts et al (1990) report regression equations (Table 1) which relate g_s to

Table 1
Linear regression statistics for stomatal conductance (mmol m^{-2} s^{-1}) with specific humidity deficit (g kg^{-1}) in five radiation classes for five canopy levels

Solar radiation class (W m^{-2})	Canopy Level	Offset	Slope
700–1000	1	459	−23 2
	2	259	−12 0
	3	244	−10 8
	4	204	−10 8
	5	244	−10 8
600–700	1	327	−12 4
	2	208	−8 8
	3	244	−10 8
	4	204	−10 8
	5	244	−10 8
500–600	1	310	−13 2
	2	226	−11 6
	3	254	−14 0
	4	214	−14 0
	5	254	−14 0
400–500	1	313	−12 8
	2	194	−12 8
	3	175	−7 6
	4	135	−7 6
	5	175	−7 6
0–400	1	233	−7 6
	2	137	−8 0
	3	133	−6 0
	4	133	−6 0
	5	133	−6 0

specific humidity deficit at all five canopy heights for a range of above-canopy radiation classes When calculating transpiration from the forest canopy, the appropriate values of stomatal conductance were calculated for each canopy level from these equations using values of above-canopy solar radiation and specific humidity deficit

Boundary-layer conductance

Boundary-layer conductance (g_a) was also determined throughout the forest canopy by Roberts et al (1990), using measurements of weight losses from wetted paper leaf replicas g_a increased sharply from the forest floor to the top of the canopy, a change expected as g_a increases with higher wind speeds However at any particular canopy level there were insufficient data to allow a definition of any subsidiary relationship between g_a and wind speed For the purposes of calculating transpiration in this study a fixed g_a value has therefore been selected for the appropriate level from the profile given by Roberts et al (1990), and this value is given in Table 2 These values retain the discontinuity in g_a noted by Roberts et al (1990), with g_a greater at 20 m than higher in the canopy at 30 m The value of g_a is multiplied by the value of L^* appropriate to each level to give g_a used in Eq (1)

Leaf area index

Derivation from literature
Estimates of leaf area index (L^*) and its vertical distribution for forest sites near Manaus were derived from data previously published by Klinge (1973) and Klinge et al (1975), as shown in Table 3 Klinge et al (1975) provide information on the distribution of leaf fresh weight in six canopy strata The assumption is here made that the dry weight of the foliage constitutes 50% of fresh weight The leaf dry weight in each stratum is then converted to L^* using values for specific leaf area given by Medina and Klinge (1983)

The vertical canopy distribution derived from data given by Klinge (1973)

Table 2
Boundary-layer conductances g_a, (mmol m^{-2} s^{-1}) at five canopy positions for the forest at Reserva Ducke

Canopy level	Height (m)	g_a
1	35 7	1320 (242)
2	30 5	960 (223)
3	23 2	1040 (175)
4	13 4	800 (93)
5	1 5	240 (28)

Values in brackets represent one standard deviation

Table 3
Derivation of Leaf Area Index (L^*) in six canopy layers in a Terra Firme rainforest near Manaus

Canopy Layer	Height (m)	Dry weight (kg ha^{-1})	Specific leaf area (cm^2 g^{-1})	L^*
A	23 7–35 4	1150	55	0 63
B	16 7–25 9	3550	65	2 31
C1	8 4–14 5	1950	75	1 46
C2	3 6–5 9	1000	85	0 85
D	1 7–3 0	1100	95	1 04
E	0 1–1 0	300	105	0 31

Data drawn from Klinge (1973) Klinge et al (1975) Medina and Klinge (1983)

and Klinge et al (1975) was allocated to five canopy layers as shown in Fig 1(a) which also shows the measurement points of the micrometeorological profile For the middle three layers of the canopy, Levels 2, 3 and 4 the measurements are made in the middle of the layer, but towards the base of the layer in the highest and lowest layers, Level 1 and 5 Figure 1(b) shows the downward cumulative distribution in the forest canopy of L^*, the total being 6 61

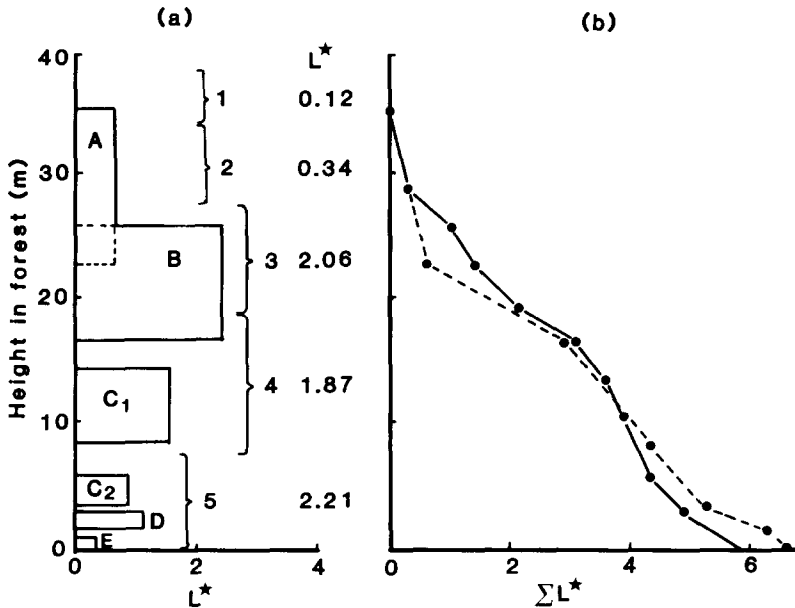Conceicao (1977), also working in the Manaus region, derived a value of 6 6

Fig 1(a) Distribution of leaf area index derived from literature values (Klinge, 1973, Klinge et al, 1975) (b) Comparison of cumulative leaf area index (L^*) used in CLATTER (● - - - ●) and that from McWilliam et al, 1993 (●——●)

for L^* from measurements of radiation interception by the forest canopy assuming a value of 0 65 for the extinction coefficient, k Recently McWilliam et al (1993) made direct determinations of L^* for a height profile through a forest 60 km from the Reserva Ducke which had been selected to be on the same part of the toposequence as this experimental site in the Reserva Ducke The total L^* they report is 5 7 ± 0 5, and shows a similar cumulative vertical distribution to that derived here from earlier literature (Fig 1(b)) The lower value of total L^* reported by McWilliam et al (1993) may well reflect the fact that their determination was made at the end of the dry season when leaf fall is at a maximum in the central Amazon The values of specific leaf area determined by McWilliam et al (1993) also compare well with those used here, see Table 3

Determination of L^* *from litter fall*

The magnitude of L^* was also determined from measurements made of areas of fallen leaves collected in 20 litter trays (0 11 m^2) at approximately every 2 weeks between July 1984 and July 1986 After collection in the forest and surface drying, the area of litter leaves was determined with a LI-3100 (Licor, Lincoln, NE) leaf area machine Figure 2 shows that the cumulative litter L^* collected over this 2 year period was 12 2 suggesting that L^* is on average 6 1

Clearly there is a good deal of consistency in these values However, the underlying philosophy of the present modelling studies is to explore the extent to which published data on physiological behaviour, canopy quantities and
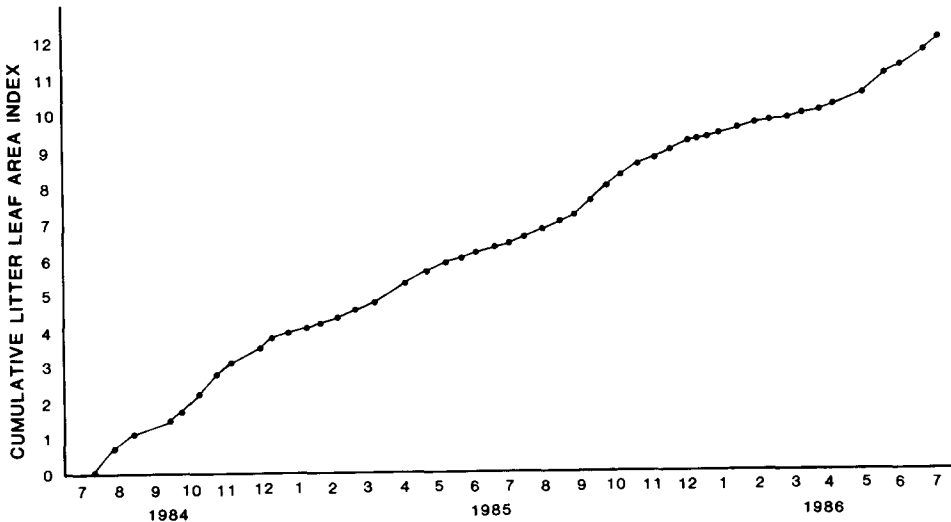

Fig 2 Cumulative litter leaf area index for the Reserva Ducke site, 1984–1986

forest microclimate can be used to estimate transpiration Consequently the L^* values used here in CLATTER are those derived from the studies reported by Klinge (1973) and Klinge et al (1975) In view of the peak of litterfall in the dry season L^* for inputting into CLATTER for September 1983 was reduced by 20% in all canopy layers

Model sensitivity

Investigations were made of the sensitivity of the calculated transpiration from the CLATTER model to changes in the input variables net radiation (R_n), specific humidity deficit (δq), air temperature (T_a), surface conductance (g_c) and boundary-layer conductance (g_a) Values were changed independently in steps of 5% from 25% below to 25% above the original values

Direct measurements of transpiration

Direct measurements of transpiration were provided by the 'Hydra', a battery-powered eddy correlation flux measurement device mounted above the forest at a height of 48 4 m The 'Hydra' system consisted of a ventilated sonic anemometer, a single beam infrared absorption hygrometer, a thermocouple thermometer and two Gill propeller anemometers Further details of this measurement system, and procedures used in data processing are given by Shuttleworth et al (1984a) For the purposes of this study the hourly average of latent heat flux measured by the 'Hydra' in dry conditions, viz the transpiration, were used for comparison with calculated values given by CLATTER, and simplified versions of that model

Model simplification

The same 'Hydra' data were used both to evaluate the performance of CLATTER and a series of simpler models to assess the level of simplification able to calculate transpiration to an acceptable level
Four alternative models were evaluated in each of which the canopy is represented as a single layer from which transpiration is calculated using the Monteith–Penman formula The entire canopy, absorbing 97 5% of net radiation is treated as a single layer with L^* equal to 6 6
Four separate models were evaluated, as follows

Model 1
In this model g_s and g_a of each canopy layer are multiplied by the value of L^*, for each canopy layer and the resulting conductances summed for use in a single-layer form of Eq (1) Air temperature (T_a) and humidity deficit (δq) required for the equation are mean values derived from five measurement levels in the forest
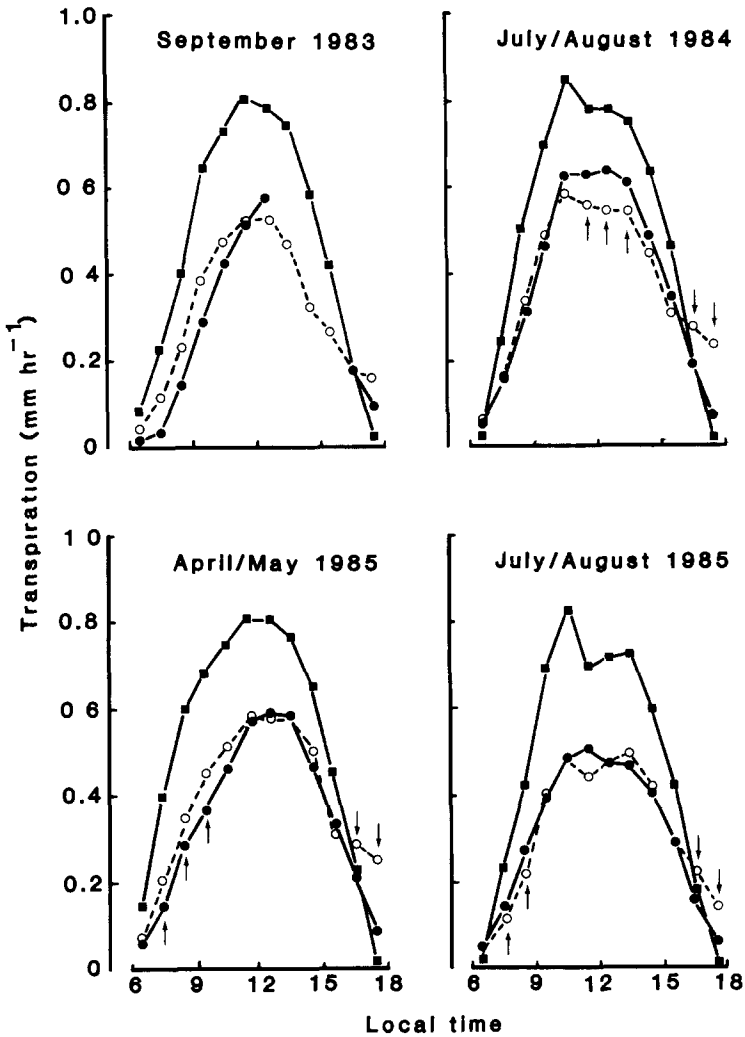
Fig 3 Comparisons of hourly transpiration measured by an eddy correlation device 'Hydra' (● —— ●) and estimated from CLATTER (○ - - - ○) for four measurement periods at the Reserva Ducke, Manaus, Brazil Where the standard errors of values differ this is indicated by an arrow Net radiation averaged for the same hours, expressed as a transpiration equivalent, is also shown (■)

Model 2

This model is identical to Model 1 except that the average through-canopy values for T_a and δq are replaced by the measured above-canopy values

Model 3

For this model g_s and g_a for all five canopy levels are first averaged and then

Table 4
Mean daily transpiration rates (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

Period	Hydra	Model
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

multiplied by the total value of L^* The resulting canopy conductances are
used in Eq (1), with T_a and δq specified as the average values from five canopy
levels as in Model 1

Model 4

This model is identical to Model 3 except that the measured above-canopy
values of T_a and δq are used instead of the average through-canopy values

Results

Model Performance

Calculations were made of hourly transpiration using CLATTER for four
periods, namely September 1983, July/August 1984, April/May 1985 and
July/August 1985 Figure 3 shows a comparison between hourly transpira-
tion averaged for several days compared with the measured transpiration
given by the 'Hydra' eddy correlation device for the same periods

There is good agreement between measured transpiration and that esti-
mated by CLATTER, although there is a tendency for CLATTER to over-
estimate transpiration at the ends of the day One explanation for this
overestimation is that CLATTER makes no allowance for the fraction of
net radiation lost as heat storage in the forest biomass, or in the air within
the trunk space Moore and Fisch (1986) estimated that the hourly energy flux
into and out of storage is frequently above 50 W m^{-2}, but sometimes reaches
80 W m^{-2} in the early morning and late afternoon, and may constitute over
50% of the net radiation at these times The hourly differences in transpiration
measured by the 'Hydra' and that estimated by CLATTER on some occasions
exceeds 0 1 mm h^{-1}, which is equivalent to 70 W m^{-2}

Table 4 shows the mean daily transpiration totals estimated from the
CLATTER and that measured by the 'Hydra' for the four 16 periods and,
apart from the 1983 values, the correspondence is excellent The numbers of

Overall daily average contribution to
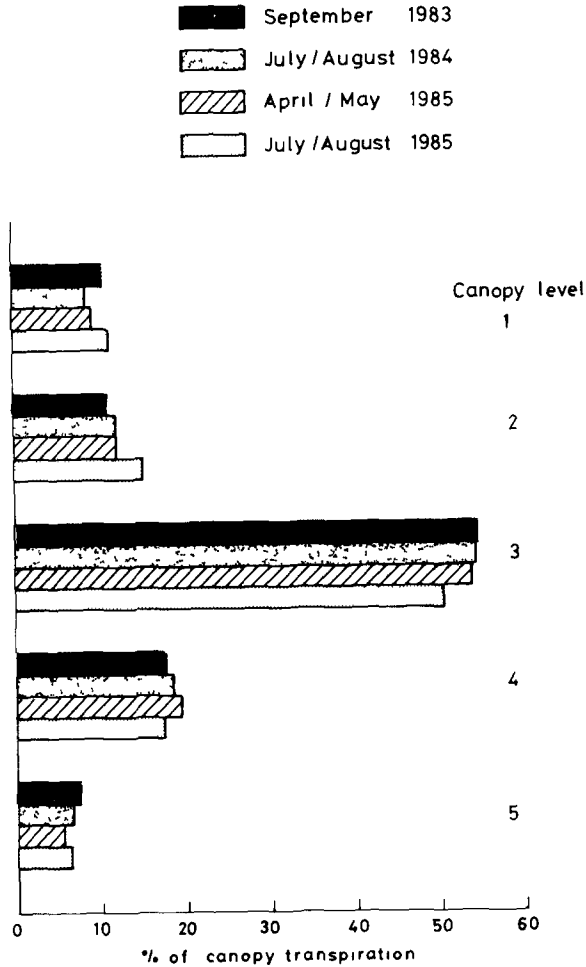canopy / transpiration

Fig 4 Estimates of the distribution of total forest transpiration to the five canopy layers in four measurement periods

hours data available for analysis in each period was September 1983, 15, July and August 1984, 118, April and May 1985, 97, July and August 1985, 49

Distribution of within-canopy transpiration

Estimates are available of the distribution of transpiration flux from each of
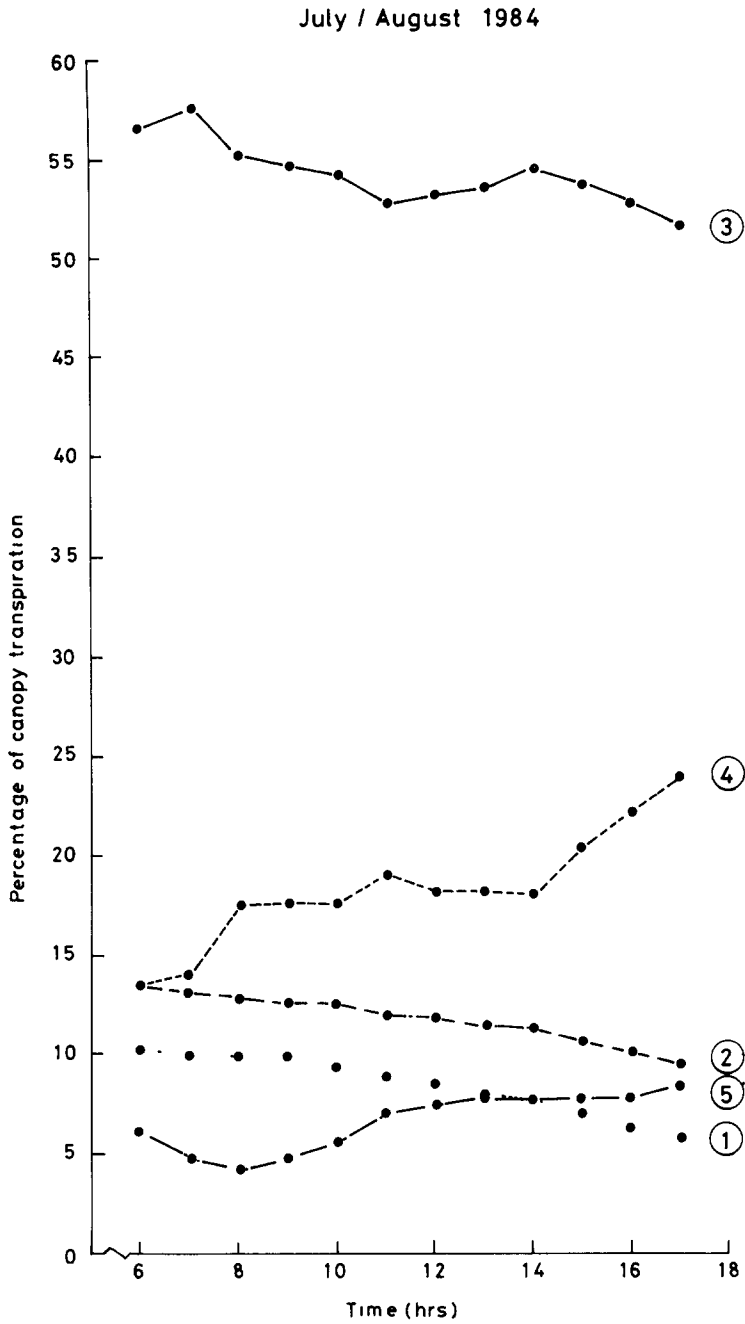
July / August 1984

Fig 5 Estimates of the diurnal trends of percentage contribution of individual canopy layers to total canopy transpiration during July/August 1984

the five forest canopy layers for each of the four study periods The distribution of L^* and the absorption of available energy through the canopy do not change in CLATTER from one period to the next so little variation in the relative contributions of each canopy layer is expected (Fig 4) The middle layer of the canopy, which has the largest fraction of L^* and has the greatest absorption of available energy, is calculated to contribute over 50% to the total canopy transpiration

Figure 5 shows hour by hour estimates for each of the canopy layers for one of the study periods, and indicates a small percentage fall in the contribution of the three upper canopy layers during the day, while the contribution from the lowest two layers rises These changes in contribution are a consequence of
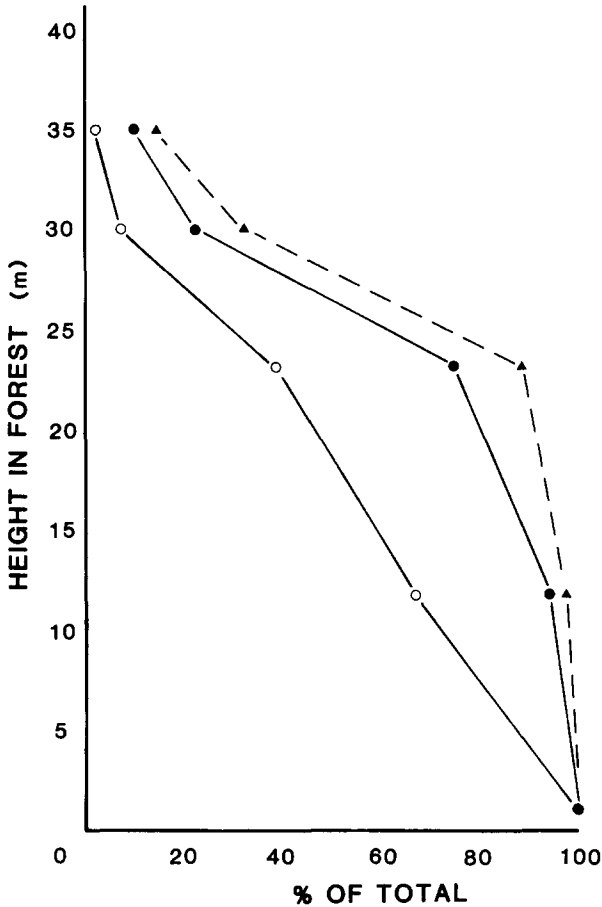
Fig 6 A comparison of the vertical downward distribution of cumulative leaf area index (○ —— ○), transpiration (● —— ●) and absorbed radiation (▲ - - - ▲) for the forest at the Reserva Ducke, Manaus, Brazil

the fall in g_s in response to atmospheric humidity deficit which is known to occur most markedly in the upper canopy (see Table 1), and is most obvious in the mid-afternoon when humidity deficits are greatest

The calculation of the net radiation allocated to each canopy layer is a function only of the L^* and its vertical distribution and the light extinction coefficient Figure 6 shows that there is close similarity between the calculated pattern of cumulative canopy transpiration and that of absorbed radiation, though less similarity with cumulative L^*

There is scope for improving the calculation of net radiation absorption since it is an important control on canopy transpiration, but CLATTER is conceived to be as simple as possible because it is unlikely that data from other tropical forest studies would have the detailed information required Studies of the sensitivity of radiation absorption of different canopy properties are rare, but a recent study by Wang and Jarvis (1990) showed that, for a coniferous forest canopy, L^* and its distribution are important but that crown shape and leaf inclination angle are less so

Figure 7 shows the sensitivity of the transpiration calculated by CLATTER to the values of the conductances g_c and g_a There is clearly a significant
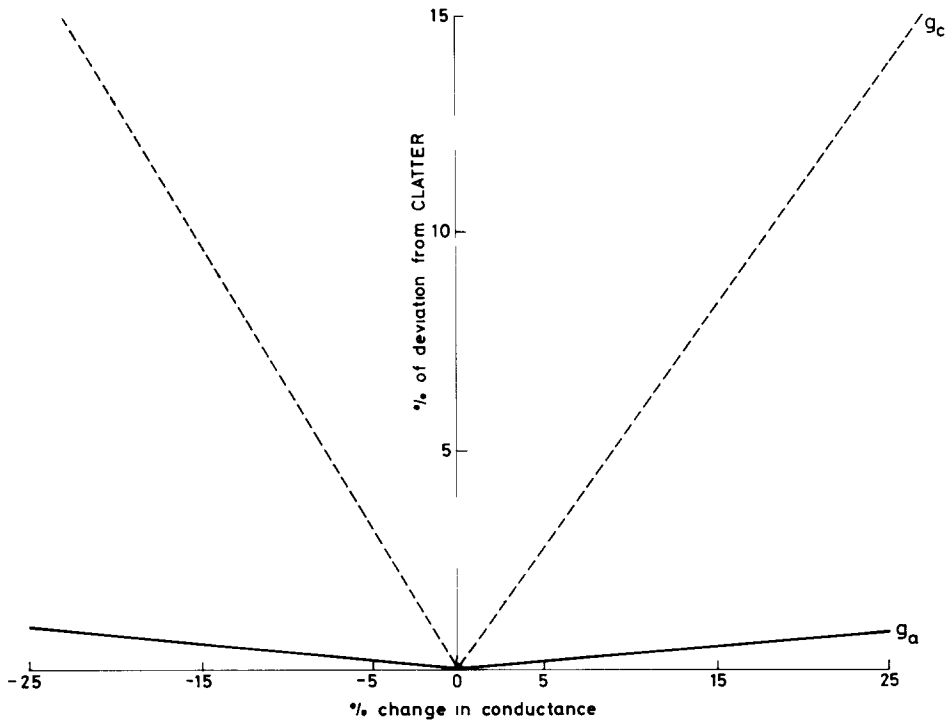

Fig 7 Sensitivity of transpiration estimated from the CLATTER model to changes in surface conductance (g_c) and boundary-layer conductance (g_a)

sensitivity to the value of the surface conductance (g_c), and hence to the value of leaf area index, L^*, or the stomatal conductance, g_s In contrast the calculated transpiration is insensitive to the value of the boundary-layer conductance, g_a Examination of the sensitivity of the estimated transpiration to the meteorological variables (Fig 8) shows that uncertainties in the value of net radiation are more important than are those in specific humidity deficit or temperature

Figure 9 shows comparisons between transpiration measured using the 'Hydra' and that estimated from five different transpiration models, including CLATTER While the agreement between measured transpiration and that estimated by CLATTER is good, progressive simplification of the calculation procedure clearly leads to larger discrepancies with respect to measured transpiration The simplest model, Model 4, in which g_s is averaged through the canopy, then multiplied by the total L^*, and transpiration calculated using weather variables measured above the canopy, produces estimates of transpiration considerably larger than those measured Less simple models, particularly those using an average of the measured microclimate through the canopy, give agreement with measurements, but do not match the comparison given by the full canopy transpiration model The regression statistics for the relationships between measurements of transpiration made with 'Hydra' and those estimated by CLATTER and the four simplified models are given in Table 5
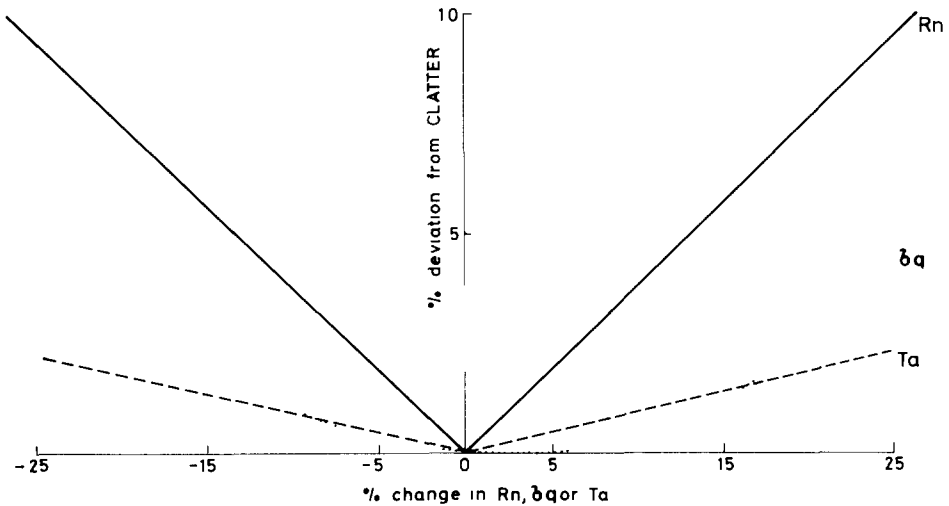

Fig 8 Sensitivity of transpiration estimated from the CLATTER model to changes in net radiation (R_n) specific humidity deficit (δq) and air temperature (T_a)
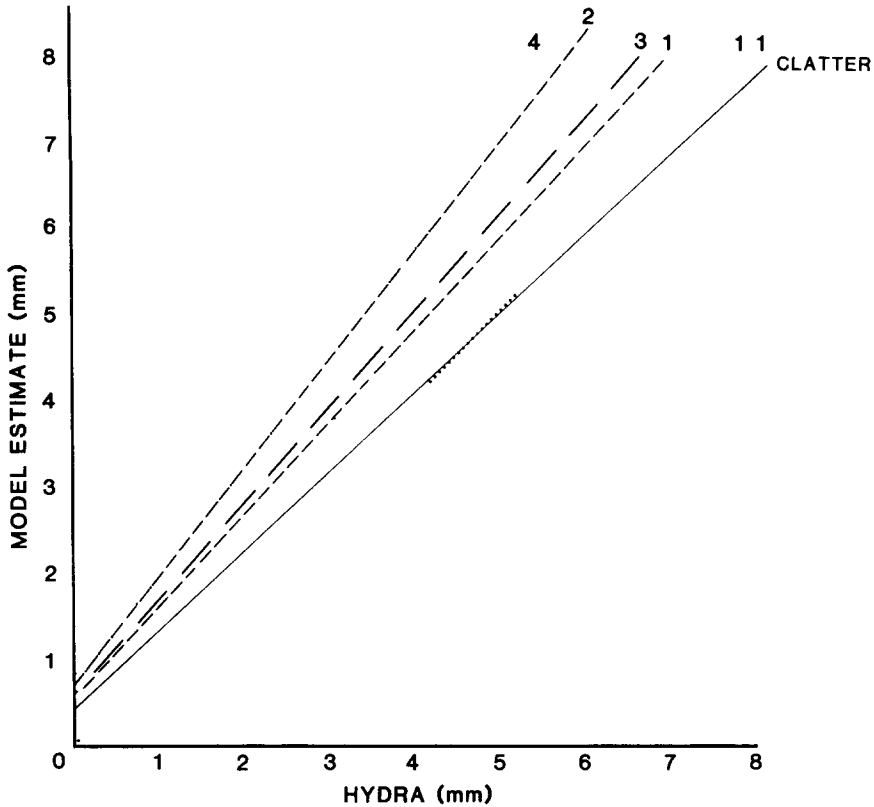
Fig 9 Comparison of transpiration measured with an eddy correlation device, Hydra` with that estimated by CLATTER and four simple derivatives of CLATTER, Models 1–4 (see text for details)

Discussion

The studies reported here clearly show the ability successfully to combine physiological data taken in a complex forest canopy with within and above-canopy measurements of the forest microclimate to provide valid estimates of forest transpiration The estimates from a multilayer calculation, such as CLATTER, for periods as short as an hour show systematic error Longer term estimates, such as over a day or week, are more accurately predicted, and this suggests such calculation procedures may well have considerable value A major constraint in using the multilayer model for other tropical rain forests is the high demand within the model for detailed physiological and microclimatic data

Simplifying the model by limiting the amount of required information on L^* distribution through the canopy, and using single point values for weather variables, proved unsuccessful in this case In less complex forest canopies the

Table 5
Regression statistics for transpiration (ı) estimated from a canopy transpiration model and simplified derivatives in comparison with measured values (ı) from an eddy correlation device Hydra

Model	Equation	r^2
CLATTER	ı = 0 456 + 0 896ı	0 93
	(0 140) (0 044)	
1	ı = 0 611 + 1 049ı	0 92
	(0 169) (0 052)	
2	ı = 0 581 + 1 110ı	0 93
	(0 164) (0 052)	
3	ı = 0 731 + 1 258ı	0 91
	(0 220) (0 069)	
4	ı = 0 773 + 1 311ı	0 92
	(0 214) (0 067)	

Numbers in brackets are standard errors for intercept and slope Both ı and ı are in millimetres per day

data requirements are much less stringent Roberts and Rosier (1993) for example, using data from Eucalyptus plantations in South India, found little difference in calculated transpiration between the multilayer calculation of CLATTER and the simpler calculation procedures used here The simpler model was justified in that case because there were only small differences in g_s through the Eucalyptus canopy This meant that the g_s from any of the canopy layers could be multiplied by the total L^* to give the canopy conductance, g_c Moreover, the canopy was open and well-ventilated, and only small gradients of temperature and humidity deficit exist, thus justifying the use of single, above-canopy values of these variables

In the present study the very detailed information on within-canopy conductances and microclimate arise from a comprehensive, multidisciplinary experimental programme, and such sets of data are rare This implies that a multi-layer calculation such as CLATTER will have only a limited role in predicting the transpiration of tropical forest using pre-existing published data This is not necessarily the case since, in the decade since the review by Doley (1981), a substantial number of reports have appeared giving information on aspects of the physiological behaviour of tropical forest species Detailed examination of this information is now warranted, particularly with regard to the magnitude of stomatal conductance and its functional relationships to weather variables such as solar radiation and vapour pressure deficit In contrast, much less new data has emerged on L^* and on its vertical distribution in tropical forests, and on the behaviour of microclimate through forests It is the shortage of this type of information which most seriously limits the usefulness of through canopy calculation models such as CLATTER However, it may well be possible to determine the form of the within-canopy normalised profiles of parameters such as temperature and

humidity deficit as empirical functions of the parameter measured over the forest or in a nearby clearing, an approach which seems likely to be a worthwhile research area for the future

In recent years, measurements of temperature and humidity deficit gradients through vegetation canopies have recorded the existence of upward fluxes of latent heat which are counter to the measured gradients inside the canopy (e g Denmead and Bradley, 1985), implying that concentration gradient, diffusion theory (K theory) is not appropriate to describe exchange processes within canopies (e g Raupach and Finnigan, 1988, Raupach, 1989) This is not a problem in the present case for CLATTER (in which the traditional gradient diffusion mechanism is assumed), because measured values of temperature and humidity deficit are used to calculate transpiration at each level There is, therefore, no need to separately model to predict these variables, see, for example Raupach (1989) Such predictions of within-canopy microclimate would be preferable, and may be necessary, in situations where data are not as complete as in this study This remains to be evaluated

Because there is good agreement between the values of transpiration estimated by CLATTER and those measured, it is not surprising that an estimate of the proportion of net radiation used in transpiration process using CLATTER compares well with measured ratios reported by Shuttleworth et al (1984a) and Shuttleworth (1988), who report between 75 and 80% for non-rainy days When calculated over the daylight periods for the 37 days for which CLATTER calculations were made in this study an average of 74 5% of the net radiation was required for transpiration This is a relatively high value, but not unique to tropical forests Rauner (1976), for instance, gave data for temperate broadleaf stands, some of which equalled rainforest in terms of the percentage of net radiation used in transpiration In contrast rates for coniferous forests may reach this high value only in the first part of the day, but never reach the same proportion on a daily basis (Jarvis et al , 1976) and Stewart and Thom (1973) show the ratio to be as low as 40% for Scots Pine in Thetford Forest, UK In this latter case the low value was simply owing to an inherently low surface conductance, and not necessarily associated with a high soil water deficit However, in other studies depletion of soil water reserves is associated with lowered use of net radiation for forest transpiration Roberts and Rosier (1993) also estimated transpiration for Eucalyptus stands in South India and, when these were well supplied with soil water, 78% of the net radiation was used for transpiration, even though L^* was only one third that of the present rainforest However, this ratio fell to only 17% when the soils were dry

Shuttleworth et al (1984a), commenting on their micrometeorological measurements of transpiration, stated that the proportion of net radiation used for transpiration by a rainforest which is almost always well supplied with water is rarely if ever more than 75% While Jarvis et al (1976) note that

for irrigated farm crops the Bowen ratio is usually close to zero, implying that almost all the net radiation is used for transpiration The conclusion then, is that even moist rainforest still exerts substantial stomatal control on transpiration, a conclusion which the direct observations of g_s Roberts et al (1990) confirm These last authors drew attention to the fact that typically values of g_s for tropical trees are not particularly high, except for the large-leaved species *Gmelina* and *Tectona* studied by Whitehead et al (1981) and Grace et al (1982) Studies of leaf water and osmotic potentials in upper canopy trees at the current Reserva Ducke study site have shown that leaf water potential can almost reach $-4\ 0$ MPa in the emergent species *Piptadenia suaveolens* and up to $-3\ 6$ MPa in *Bocoa viridiflora* an upper canopy species (J Roberts and O M R Cabral, unpublished data, 1984) These values, which are taken in mid-afternoon, are close to the turgor loss point for leaves, hence plants lowering the value of g_s to restrict transpiration and prevent leaf dessication clearly has an important role, even though soil water supply is apparently not limiting

The upper canopy layer of this forest had an L^* of 0 12 and is treated as an horizontally homogenous entity in CLATTER This is a simplification as this canopy layer comprises the crowns of emergent trees which are spatially separated This will mean that the absorption of net radiation by trees in this layer and consequently the radiation levels reaching the layer below will be a function of the dimensions of the emergent trees' canopies, the spacing between emergent trees and sun angles Because of the rather low level of L^* in the upper canopy layer no attempts have been made to account for the spatial heterogeneity in the 24 upper canopy level within CLATTER However, the configuration of emergent tree canopies can vary widely between rain forests and it is planned that derived versions of CLATTER will take account of discontinuous upper canopy layers Physiological and micrometeorological data are becoming available for this development from a study in a rain forest near Maraba, Para, Brazil This is one of the rain forest sites of the ODA-supported ABRACOS (Anglo–Brazilian Amazonian Climate Observation Study) project operated by the Institute of Hydrology and collaborating Brazilian institutes A particular feature of this forest are Brazil nut trees (*Bertholletia excelsa*) which largely compose a distinct emergent layer The horizontal spatial separation between individual emergent trees is much greater than observed at the Reserva Ducke, Manaus The Brazil nut trees can have crowns up to 70 m in diameter and are roughly spherical in shape Preliminary observations show that above-canopy radiation is substantially attenuated by these densely foliated crowns leading to a large variation in the radiation reaching the sub-emergent tree layer In this case it will be necessary to use a more sophisticated treatment of radiation absorption by the upper canopy layer in CLATTER

In summary, the main points arising from this study are that through

canopy calculations of transpiration from basic plant physiological and microclimatic information closely matches measured whole canopy transpiration, but that calculations made with simpler models are less good

Conclusions

The multi-layer canopy transpiration model (CLATTER) gives good prediction of transpiration from tropical rain forest when compared with the eddy correlation device 'Hydra' on an hourly basis There is however divergence early and late in the daylight period probably because CLATTER makes no allowance for changes in heat storage in the forest Averaging over daily periods improves the prediction of transpiration such that estimates from CLATTER and 'Hydra' measurements differ by only a few percent

The rigour of the model supports the assumptions made in it namely the values of fresh to dry weight ratios and specific leaf areas used to derive a canopy profile of L^* from literature values and the extinction coefficient of net radiation extinction (0 6) which was used Studies of the sensitivity of CLATTER to likely errors of inputted variables revealed the greater importance of g_s, L^* and R_n with δq and T_a less important CLATTER is insensitive to large errors in g_a

The data requirements for CLATTER could not be reduced without generating overestimates in transpiration The most simple model which uses canopy averages of stomatal and boundary-layer conductances multiplied by total L^* and above-canopy values only of δq and T_a overestimated transpiration by up to 50%

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