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Micrometeorology of Temperate and Tropical Forest [and Discussion]

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Micrometeorology of temperate and tropical forest

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The literature on the micrometeorology of temperate and tropical forests is reviewed to determine whether structural or species difference between these biomes alters their interaction with the atmosphere. Considerable consistency is found in the value of those whole-canopy features of most importance to this interaction, namely solar-reflection coefficient, through-canopy radiation absorption, aerodynamic roughness, the symptoms of near-surface *K*-theory failure, the canopy store for rainfall interception and the magnitude and environmental response of their bulk stomatal (surface) resistance. Typical values of these parameters and functions are given with a view to their potential use in climate simulation models. Attention is drawn to the fact that this similar micrometeorological response can generate different time-average surface-energy partitions when interacting with different climates and, in particular, alters between the edge and the middle of continents. This is of considerable significance, implying tropical deforestation is likely to have most effect on river flow (though not climate) at continental edge and island locations. The similar micrometeorological response of forests is interpreted as the necessary consequence of energy and mass (water) conservation acting as an area average on vegetation that is, by definition, dense and extensive, to reconcile a characteristically tall growth habit with a perennial nature.

1. Introduction

Forest micrometeorology is the study of the interaction between extensive areas of dense vegetation, comprising mainly tall woody plants, and the atmosphere that permeates and immediately overlies it. For vegetation to be defined as a forest it is not necessary that it consists entirely of trees, though these should play a predominant role; it is, however, necessary that the vegetation be sufficiently dense that the individual interaction of each plant with the atmosphere is influenced by that of its neighbours. Above the ground such influence occurs through the environment to which separate plants are exposed, in particular electromagnetic radiation and temperature, humidity and wind speed of the air. Below ground, interaction occurs as the root systems compete for available resources, particularly water and nutrients, stored in the soil.

Micrometeorologists study the interaction of the three-dimensional components that constitute a vegetation stand, to improve the definition of the most important physical and physiological processes involved. However, when describing a complete canopy, they usually constrain the representation to one dimension, sacrificing precision for generality if required. This attitude is reflected in the format of experimental studies in forest micrometeorology, and in the structure of this paper.

Earlier papers presented at this meeting (Leuning; Raupach; Black) give detailed attention to aspects of the vegetation–atmosphere interaction inside forest canopies. Later papers (de Bruin & Jacobs; Andre *et al.*; Dickinson) consider the consequences of the whole-canopy behaviour of forests on meteorology at increasing area scales. Because micrometeorology is concerned with both in-canopy and whole-canopy behaviour, my paper provides continuity between these contributions. The particular perspective adopted here is to compare the micrometeorology of temperate and tropical forest stands.

2. Temperate and tropical forest stands

Since micrometeorological experiments on forests first began, finance and practicality have dictated that most of these experiments were done in temperate latitudes (see, for example, Black & McNaughton 1971; Stewart & Thom 1973; McNeil & Shuttleworth 1975; Gay & Fritschen 1979). Recently, such studies have been complemented with similar work in tropical forests (see, for example, Pinker *et al.* 1980*a*, *b*; Shuttleworth *et al.* 1984*a*, *b*; Monteny 1987; Shuttleworth 1988; Lloyd & Marques 1988; Lloyd *et al.* 1988).

Tropical and temperate forests share four properties that are very significant in their interaction with the atmosphere: they are extensive, dense, tall and perennial. In other regards they are dissimilar, particularly those forest stands that have been subject to micrometeorological investigation.

Their definitive characteristic is geographical location. Within the physiognomic classification of natural vegetation given by Kuchler (1949, 1983), tropical forests are conveniently classified as evergreen broadleaf (group B). In the same way, temperate forests are classified as deciduous broadleaf, evergreen needleleaf, mixed deciduous broadleaf/evergreen needleleaf and deciduous needleleaf (groups D, E, M and N, respectively). The location of these groups is mapped in figure 1.

Being located near the equator, tropical rain forests receive plentiful radiation, and they occur where there is adequate, though perhaps seasonal, rainfall. They do not normally experience (even intermittent) climatological extremes. Temperate forests, on the other hand, have a harsher and more problematic existence, and are located where man first undertook massive exploitation and management. In consequence, temperate forests generally contain fewer tree species than tropical forests, and are often monocultures. This may be the result of selective pressure, but is often merely the result of human intervention.

That growing conditions are persistently favourable means evergreen broadleaved forest generally sustains a high leaf area per unit ground area (leaf area index), typically in the order 5–10 (Medina & Klinge 1983). Individual trees exhibit seasonal leaf fall, but the total leaf cover is maintained high, and leaf activity vigorous. Temperate, deciduous forest, however, has a distinctive change in seasonal leaf cover, and even evergreen temperate forests exhibit seasonal changes in leaf area and leaf vigour. With sustained growth and no recurrent human intervention to shorten the natural growth cycle, tropical forests tend to be (say) 30% taller and to have larger woody biomass than managed temperate stands.

Undisturbed tropical rain forests usually present two to four distinguishable strata. The major leaf area accumulates in the upper and middle canopy, but there is a substantial amount of leaf in the lower stratum of the forest (Medina & Klinge 1983). In many temperate coniferous canopies the leaf area follows a normal distribution in the vertical between the top of the tree and the base of the live crown (Jarvis & Leverenz 1983). There is less regularity in the vertical distribution of foliage in deciduous broadleaved forests, but a distinct, elevated canopy with a

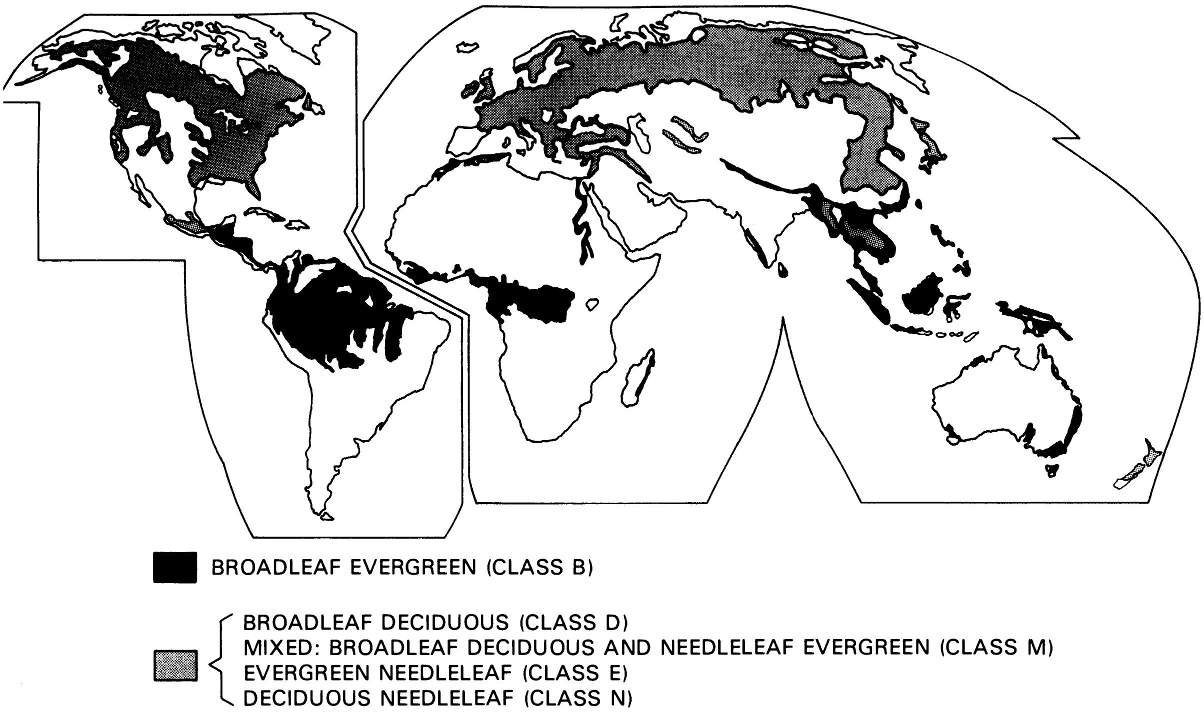

Figure 1. Classification of temperate and tropical forests adopted in this paper. Following the physiognomic classification of Kuchler (1949, 1983), temperate forests are taken as classes D, E, M and N, tropical forest as class B.

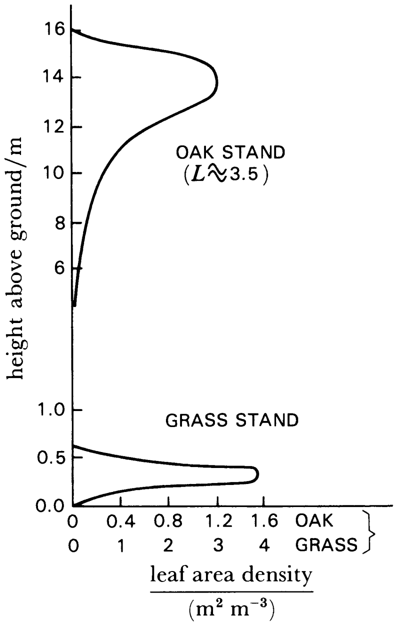

Figure 2. Leaf-area density against height for an oak forest with grass understorey, illustrating a distinct, elevated layer of tree foliage typical of many temperate stands, both deciduous and coniferous. The presence of an understorey of different species is also common for temperate stands that have a relatively small leaf-area index. (Redrafted from Rauner (1976).)

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trunk space beneath is not uncommon. Both coniferous and deciduous temperate forests with low leaf area index frequently have an understorey of a different species. Figure 2 shows an example for a 40-year-old oak stand. Forest management, in the form of planting, thinning and brashing, serves to emphasize natural concentrations in the vertical distribution of leaf area and other biomass. Such management is more common in temperate stands and can easily alter the details of in-canopy transfer and affect measured profiles of atmospheric variables within the canopy (see §5*c*).

In summary then, tropical and temperate forest stands are similar in that they are extensive, dense, tall and perennial; four aspects that are profoundly significant in their interaction with the atmosphere. They differ in that natural tropical forests are generally taller and possess more tree species than managed temperate forests. They often have larger biomass and leaf area, this last with a more uniform height distribution. The purpose of this paper is to see if these differences in degree modify the respective micrometeorological responses of these forests.

3. The framework of micrometeorological comparison

In micrometeorology, attention is primarily focused on aspects of the vegetation–atmosphere interaction that directly influence those measurable properties commonly used to specify climate in meteorology. Experiments therefore often concentrate on the exchange of energy, momentum and water, both as a liquid and as water vapour, because these have a dominant influence on the daily and seasonal weather cycle. Other important exchanges occur, particularly of aerosols and minority gases such as carbon dioxide, which may also affect climate in the longer term.

In practice the rate of interchange varies considerably with the weather and with (sometimes related) changes in plant response. To introduce consistency, time-independent models are constructed which identify and incorporate the most important physical and physiological mechanisms involved in the interaction. The submodels used to describe these mechanisms represent a subsidiary specification of the micrometeorological interaction, which arguably provides a more robust framework of comparison.

In practice, the complexity of micrometeorological models varies considerably (see, for example, Shuttleworth (1983)). The more complex but realistic the description, the more particular is the calibration required for an individual crop. This paper compares micrometeorological studies made with forest stands of different structure. Such comparison is therefore best made with reference to the most general, and hence simple, model available.

I consider some aspects in more detail, but generally consider the forest canopy as a single entity. This canopy reflects, intercepts and transmits radiation in specific proportions characteristic of the stand, and is capable of intercepting and retaining a specified amount of water during each rainstorm. A few characteristic parameters specify its aerodynamic roughness, which dictates the momentum it absorbs, and is the primary control on the turbulent transfer of sensible and latent heat between their effective source in the canopy and the atmosphere above. If the canopy is dry, transpiration is additionally restricted by molecular diffusion through the stomata: the combined effect of the stomata is represented by a canopy resistance (Monteith 1965) the value of which alters in response to changes in the atmosphere, plant and soil and is also a characteristic of the stand.

4. Radiation exchange

The exchange of radiant energy is arguably the most important aspect of the interaction between the atmosphere and any vegetation. Thermal radiation transfer in forest canopies is simplified by the efficient turbulent transfer of sensible heat, described in §5, which maintains the surface temperature of the vegetation close to air temperature (see, for example, Shuttleworth (1976*b*)). During the day the long-wave emission of forests might well be systematically less than for other vegetation types for this same reason (Rutter 1968). It is a characteristic of forest stands that they capture more solar radiation than other vegetation, and this is a more significant factor in increasing the net input of radiant energy.

4*a*. *Solar reflection coefficient*

The leaf area of the canopy, the spectral properties of the leaves, and their size, shape and orientation all affect the bulk transmission and reflectivity of forest vegetation (Jarvis & Leverenz 1983). However, perhaps the characteristic feature of forest canopies most responsible for the enhanced capture of solar radiation is the distribution of the interacting foliage, and the fact that this is clumped in tree crowns. Secondary clumping around shoots and branches assists (Baldocchi *et al.* 1985), but the presence of organized peaks and depressions in the upper surface of forest vegetation ensures that much of the incoming solar radiation is already well below the top of canopy before it undergoes its first optical scattering. The relative depth and separation of such surface irregularities is associated with the overall scale of the plants that make up forests. The ensuing enhanced efficiency in solar radiation (and indeed momentum) capture is therefore inherent to forest vegetation.

Notwithstanding the comments of the previous paragraph, the total hemispherical reflection coefficient for solar radiation, the so-called albedo, and its dependence on solar elevation, varies in significant detail from one forest canopy to the next. In a review of studies of coniferous forest stands, Jarvis *et al.* (1976) reported values of the reflection coefficient measured around midday: the mean and standard deviation is 0.117 ± 0.032. This value, which is arbitrarily assumed to correspond to a solar elevation of 45° for plotting purposes, is shown in figure 3*a* along with the solar elevation dependence observed for one particular spruce canopy. The observed shape of this last function varies, but the weak dependence at all but low solar elevation and the change with cloud conditions is typical. This restricted daily range in reflection coefficient is probably also, in part, related to the characteristic clumped nature of forest foliage.

Figure 3*a* also illustrates the change in albedo for an oak forest (Rauner 1976), and a value of about 14% has been reported at high solar elevations in a mixed oak–hickory forest (Baldocchi *et al.* 1985) and a birch–aspen forest (Rauner 1976), both in full leaf. The measured albedo is lower in the absence of foliage and this may be evidence that enhanced solar entrapment is primarily associated with physical structure, but it is also partly related to the different optical properties of trunks, branches and ground litter. The presence of deciduous foliage in the summer months clothes the canopy in more reflective optical elements, often with an orientation that is biased towards the horizontal, and which moderates the topography of the canopy top; all of these tend to increase the solar reflectance. In temperate latitudes the presence of snow on the canopy and ground during winter can dramatically increase the albedo of both evergreen and deciduous forest.

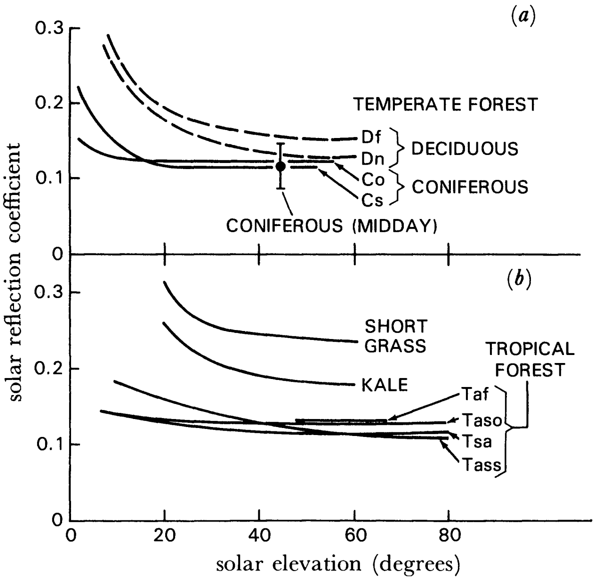

Figure 3. Solar reflection coefficient plotted against solar elevation (*a*) for temperate forest and (*b*) tropical forest; also shown in (*b*) are values for kale and short grass from Monteith & Szeicz (1961). The full-circle with error in (*a*) is the mean and standard deviation of midday values for temperate coniferous stands from Jarvis *et al.* (1976). Curves for the forest stands are indexed as follows: Df, deciduous, full foliage; Dn, deciduous, no foliage; Co, coniferous, overcast; Cs, coniferous, sunny; Taf, tropical, Africa (Oguntoyinbo 1979); Taso, tropical, Asia, overcast (Pinker *et al.* 1980*a*); Tsa, tropical, South America (Shuttleworth *et al.* 1984*b*); Tass, tropical, Asia, sunny (Pinker *et al.* 1980*a*).

So far, the available data from tropical forests in Asia, South America and Africa, which are shown in figure 3*b*, suggest that the albedo is more consistent than for temperate forests. Typically, values are in the range 0.12 ± 0.01, and are therefore more comparable to temperate evergreen than temperate deciduous canopies. For comparison, and to illustrate the enhanced radiation capture by all forest stands, figure 3*b* also shows curves for short grass and kale on sunny days. The value of their albedo at high solar elevation, about 25 and 18 %, respectively, is arguably typical of grassland and agricultural crops.

Computer models of global climate require a suitable definition of the large-scale average albedo for forest biomes. In the light of the above discussion, 0.12 seems to be a realistic recommendation for tropical and temperate evergreen forests, and for temperate deciduous forest in the absence of both foliage and snow cover. With full foliage the albedo of temperate deciduous stands is slightly higher, perhaps 14 %. It is probably not necessary to take account of the restricted and poorly defined response of forest albedo to solar elevation in such computer models because enhanced reflection only occurs with low incoming solar radiation. The significant energy storage in the biomass and air that constitute a forest canopy will mask any time dependence in surface energy that is the result of diurnal changes in the solar reflection coefficient. A fixed value, the measured daily average, is therefore the realistic choice.

4*b*. *Through-canopy penetration*

Most of the unreflected solar radiation incident on a forest is absorbed by the tree canopy and the remainder is transmitted to the ground or to a vegetation understorey beneath. Once the initial radiation scatter has occurred, the topography of the canopy becomes less important and the primary control on transmission through the canopy is leaf-area index, although the distribution, orientation and optical properties of the foliage are also significant (Jarvis & Leverenz 1983). Many models have been written to describe the penetration of radiation in vegetation (see, for example, de Witt 1965; Monteith 1965; Norman & Jarvis 1975; Norman 1981) but most were developed to describe uniform canopies. Some have been tested in forest stands (see, for example, Baldocchi *et al.* (1985)), and it is not certain that such modelling can yet provide a general representation that adequately describes the effect of clumped vegetation in forests.

An alternative is to express the transmittance, τ, of diffuse and solar-beam radiation through a forest canopy in terms of an empirical coefficient, B, thus:

$$\tau = \exp(-BL), \tag{1}$$

where L is the leaf-area index. An assumed logarithmic extinction of the total radiant energy by forest canopies is very often an adequate description within the considerable sampling errors associated with in-canopy radiation measurements. Equation (1) cannot, however, describe the extinction of the individual components of the radiation spectrum contributing to the total flux. Jarvis & Leverenz (1983) gave values of B for seven coniferous and six broadleaved forests. The values range from 0.28 to 0.65, with a mean and standard deviation of 0.47 ± 0.11 for coniferous stands and 0.47 ± 0.13 for broadleaved stands.

The percentage of radiation penetrating the tree canopy of temperate forests can vary widely from (say) 32% (Gash *et al.* 1988) to 1% (Norman & Jarvis 1974). Greater penetration is associated with sparse tree canopies, and very often allows a vegetation understorey that can absorb most of the remaining radiation. A typical value for the percentage of radiation ultimately reaching the ground beneath a temperate forest during summer months is 5 ± 4% (Jarvis & Leverenz 1983), which, with the mean value of B given above, would occur with an equivalent total leaf-area index of about 6. The measurements available for tropical forests (see Snedaker 1970; Pinker *et al.* 1980*b*; Shuttleworth *et al.* 1984*a*, *b*) are lower, typically 3 ± 2%, and are perhaps therefore consistent with a somewhat larger leaf-area index.

5. TURBULENT TRANSFER

The basic specification of the aerodynamic interaction of forests involves assigning values to the aerodynamic roughness, z_0, and the zero-plane displacement, d. In near-neutral conditions of thermal stability, the wind speed u, at height h above a vegetation canopy, is generally taken to have the form

$$u = u_*/k \ln[(z-d)/z_0], \tag{2}$$

where u_* is the friction velocity and k is von Karman's constant (often set as 0.4). Values of z_0 and d are usually determined by optimizing this expression against measured profiles in neutral conditions. Alternative procedures have been suggested (Molion & Moore 1983; Sellers *et al.* 1988), but these also require that d is speculatively assigned additional physical significance.

In a review of coniferous forests, Jarvis *et al.* (1976) reported values of z_0 and d relative to h for 15 stands. These vary widely, with z_0 between $0.02h$ and $0.14h$, and d between $0.67h$ and $0.92h$. The mean and standard deviations are $(0.076 \pm 0.047)\,h$ and $(0.78 \pm 0.09)\,h$, respectively. This value of the ratio (d/h) is significantly larger than that normally quoted for farm crops, namely $d \approx 0.63h$ (see Monteith 1973), whereas the ratio (z_0/h) is correspondingly smaller than that so quoted, namely $z_0 \approx 0.13h$, although in both cases $z_0 \approx (h-d)/3$. The larger value of (d/h) probably reflects the longevity of forest stands, and the ensuing tendency to have more foliage nearer the top of the canopy.

Although micrometeorological studies involving wind speed profiles adequate to estimate z_0 and d are extremely rare for tropical rain forest, two very different analyses for the same site in central Amazonia (with $h \approx 35$ m) report $z_0 = 2.2$ m and $d = 30.9$ m (Molion *et al.* 1988), and $z_0 = 2.02$ m and $d = 28.8$ m (Sellers *et al.* 1988). The difference between these two estimates is well within the variability normally found in independent single-site analyses, although in fact neither analysis used a simple optimization against profile data.

The ratios $(d/h) \approx 0.86$ and $(z_0/h) \approx 0.06$ for this forest, although within the range of values given by Jarvis *et al.* (1976) for temperate coniferous stands, are none the less larger than average for d and smaller for z_0. This is not unexpected: it may well be a characteristic difference between tropical and temperate forest stands, if the former tend to be taller and have larger leaf area.

5*a*. *K-theory failure: significance to energy partition*

'*K*-theory' is now known to be inappropriate within and just above vegetation (Raupach, this symposium). However, a simple description of the net exchange of energy between the whole canopy and the atmosphere by using expressions based on first-order closure is none the less remarkably effective (Gash & Stewart 1977; Calder 1977; Dolman *et al.* 1988; Shuttleworth 1988). This is the result of several, possibly fortuitous, numerical relations (Shuttleworth 1988), which can be summarized as follows.

1. The rate of transpiration from a dry forest canopy shows little sensitivity to the value assumed for the aerodynamic transfer resistance (Shuttleworth 1988) and is primarily related to the stomatal resistance of the canopy, this being typically an order of magnitude bigger.
2. A significant proportion (about half) of the rain water intercepted and evaporated by a forest is lost subsequent to the storm. The efficiency of turbulent transfer controls the rate of evaporation of this interception store, but has little effect on the total loss (Shuttleworth & Gash 1982).
3. For dense forest vegetation the enhanced efficiency of energy transfer above that of momentum just above the canopy (see §5*b*) and the presence of an excess resistance to energy transfer within the canopy (Chamberlain 1966; Thom 1972), act in opposite senses and can be of approximately equal magnitude.
4. In models of total evaporation, the effect of increasing the assumed value of aerodynamic resistance decreases the calculated water loss from wet canopies but gives a complementary increase in transpiration, and vice versa (see Shuttleworth 1988). This is because the within-canopy water-vapour saturation deficit calculated in dry conditions rises (see Monteith 1965, p. 222).

Despite the above, the failure of first-order closure theory adjacent to vegetation remains a problem that has stimulated considerable experimental and theoretical interest. The past 10 years have seen several field experiments over temperate forest stands (Thom *et al.* 1975; Garratt 1978; Raupach 1979; Denmead & Bradley 1985; Baldocchi & Hutchison 1987), a commensurate number of wind-tunnel studies (Raupach *et al.* 1980, 1986; Coppin *et al.* 1986; Legg *et al.* 1986), and numerous theoretical discourses on this subject (Shaw 1977; Wilson & Shaw 1977; Raupach & Shaw 1982; Massman 1987; Raupach 1987). Some agreement is beginning to emerge and aspects are discussed by Raupach (this symposium). My paper compares data now available from tropical forests, which complement those from earlier temperate studies.

5*b*. *K-theory failure: above-surface diffusion*

The transfer efficiency for scalar atmospheric constituents just above vegetation is observed to be higher than expected from *K*-theory, assuming the empirical stability correction functions previously considered to be universal. This enhancement, first reported as the 'Thetford anomaly' (Thom *et al.* 1975; Raupach 1979), seems not to occur to the same extent for momentum transfer over dense forest vegetation (Raupach 1979); but Garratt (1978) found enhancement for momentum over less dense stands. Subsequent reanalysis (Garratt 1980) suggested these observations are consistent; enhancement occurs through a transition layer the depth of which is inversely related to the separation of the trees for momentum, but is different (deeper) for scalar constituents. Clearly, tropical forests must be considered dense vegetation and compared with dense temperate forest.

According to constant flux-layer similarity theory (Monin & Yaglom 1977), the dimensionless profile gradients for momentum, temperature and water vapour above the canopy may be written as

$$k(z-d)/S_* \, \partial S/\partial z = \phi_{\mathrm{H,W,M}}(\xi), \tag{3}$$

in which S is either wind speed, u, potential temperature, θ, or specific humidity, q, at height z above the ground, and S_* is equivalent, being the friction velocity, u_*, friction potential temperature, θ_*, or friction specific humidity, q_*, respectively. These last two are defined by

$$\theta_* = H/(\rho_a c_p u_*) \tag{4}$$

and

$$q_* = \lambda E/(\rho_a \lambda u_*), \tag{5}$$

where ρ_a is the density of air and c_p its specific heat at constant pressure, λ is the latent heat of vaporization of water, and H and λE are the above-canopy sensible and latent-heat fluxes, respectively. Surface-layer similarity theory assumes that the non-dimensional functions ϕ_{H}, ϕ_{W} and ϕ_{M} depend only on the stability parameter $\xi = (z-d)/l$, where l is the Monin–Obukov length.

These functions were considered independent of the vegetation and universally defined for all heights above canopy, albeit by empirically derived functions. They have been expressed as several empirical formulae, which differ in detail but have similar form (see Thom *et al.* (1975) for examples). Significant enhancement in the reciprocal of their measured value (i.e. ϕ_{H}^{-1}, ϕ_{W}^{-1} and ϕ_{M}^{-1}) above a forest canopy corresponds to enhanced turbulent transport above that expected on the basis of similarity theory.

The data plotted as full circles in figure 4 (from Raupach 1979) are typical of those observed over (dense) temperate forest. The data plotted as open circles (with error estimate) (from Viswanadham *et al.* 1987) were collected above tropical forest in central Amazonia. The full lines in each case are the form commonly ascribed to these empirical stability functions, and are the formulae given by Dyer & Hicks (1970) for $\xi < 0$, and by Webb (1970) for $\xi > 0$.

Little significance should be given to the low values of ϕ_{M}^{-1} over tropical forest when ξ is greater than zero: a mechanical sensor was used to measure horizontal wind speed in this experiment, and u_* is particularly prone to undermeasurement in stable conditions. Otherwise, the two sets of data show adequate consistency. There is a common enhancement of about a factor two in ϕ_{H}^{-1} and ϕ_{W}^{-1} in near-neutral atmospheric stability. This persists in unstable conditions, with some evidence of reduction in the proportional increase as the atmosphere

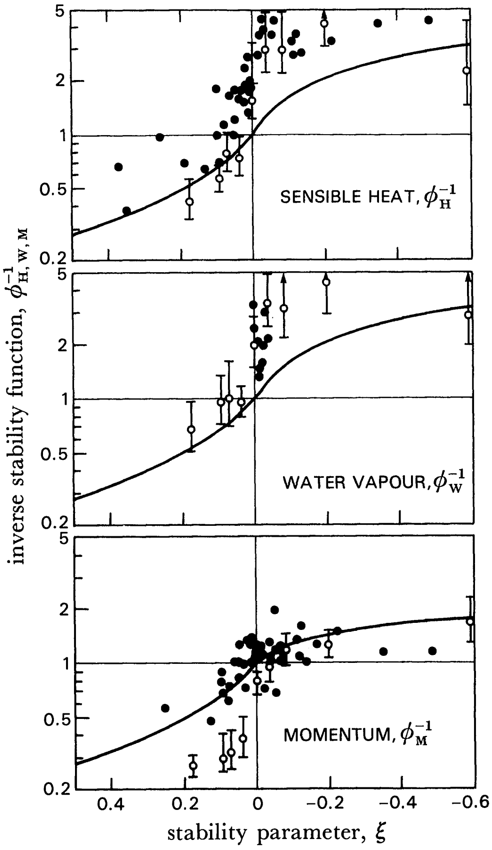

FIGURE 4. Inverse stability function $\phi^{1}_{H,W,M}$ for sensible heat, water vapour and momentum respectively, plotted against the stability factor $\xi = (z-d)/l$. The full circles are above a temperate coniferous forest of Scots pine near Thetford, England, and the open circles (with error) above a dense, tropical rain forest near Manaus, Brazil. The lines are empirical stability functions as given by Dyer & Hicks (1970) for $\xi < 0$, and by Webb (1970) for $\xi > 0$. (Temperate forest data are redrafted from Raupach (1979); tropical data are derived from Viswanadham *et al.* (1987).)

becomes more unstable. In neither case is there obvious enhancement in the stability function for momentum with a neutral or unstable atmosphere. In stable conditions, values of ϕ_H^{-1} and ϕ_W^{-1} for the tropical forest are consistent with the Webb (1970) formula within the large experimental errors: ϕ_H^{-1} for temperate forest is less obviously so.

The approximate equality between ϕ_H^{-1} and ϕ_W^{-1} implies equivalent equality in the eddy diffusivities for sensible and latent heat. Enhanced transfer just above the canopy therefore seems to occur for both energy fluxes equally within (albeit large) experimental error.

5*c*. *K-theory failure: within-canopy profiles*

The failure of *K*-theory is most obvious inside canopies with an elevated concentration of foliage. Many temperate forests have a leaf area distribution of this type and frequently provide evidence for the transfer of atmospheric entities that run counter to their equivalent vertical concentration gradient.

Early studies of wind speed profiles commonly demonstrated a definite increase in the trunk space, even at ideal micrometeorology sites (Oliver 1971). This is inconsistent with a monotonic loss of momentum through the canopy, and is indirect evidence of countergradient flow. Figure

5*a* shows an example for a temperate Scots pine (*Pinus sylvestris* L.) forest with tree foliage concentrated over the height range 8–15.5 m. The wind speed profile for undisturbed Amazonian forest given in figure 5*b* is not definitive for the existence of a within-canopy wind speed maximum. There is evidence of some reduction in the upper foliage, but the data are prone to anemometer stalling errors.

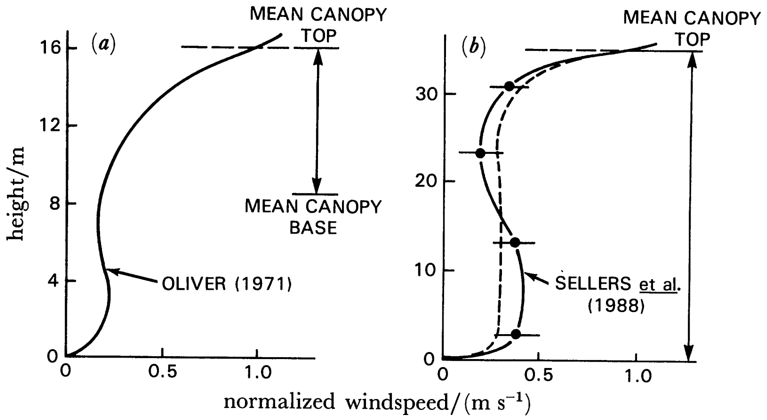

FIGURE 5. Average wind speed as a function of height normalized to that at the top of the canopy for (*a*) a temperate forest of Scots pine with an elevated foliage distribution near Thetford, England, and (*b*) a tropical rain forest with more uniform foliage distribution near Manaus, Brazil. (Part (*a*) is redrafted from Oliver (1971) and (*b*) from Sellers *et al.* (1988).)

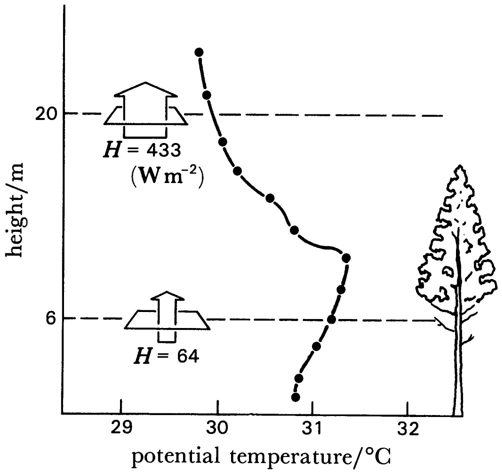

FIGURE 6. Average air temperature as a function of height through the canopy of a temperate forest of *Pinus ponderosa* with an elevated foliage distribution near Canberra, Australia; also shown are simultaneous direct measurements of sensible heat flux made at heights of 20 m and 6 m where the temperature profile has the opposite sign. (Redrawn from Raupach (1987).)

During the day, simultaneous within-canopy maxima in air temperature and humidity are a common feature in temperate forests with elevated foliage. These, in conjunction with a measured positive, below-canopy energy balance, provide indirect evidence of counter-gradient energy flow. Direct evidence was provided when such profiles were observed simultaneously with co-located, direct (eddy correlation) measurements of outward energy flux (Denmead &

Bradley 1985). Figure 6 shows an example temperature profile and associated sensible heat flux for Uriarra forest, a plantation of Western yellow pine (*Pinus ponderosa* Dougl.) near Canberra, Australia.

This feature is less apparent if the leaf-area distribution is of more uniform vertical structure because profiles then become more uniform, reflecting the progressive capture of radiation through the canopy. Figure 7 illustrates such profiles for a tropical forest in day-time and night-time conditions. There are no marked points of inflection where leaf area is largest at approximately 80% of canopy height, although there is a broad maximum in temperature through the canopy.

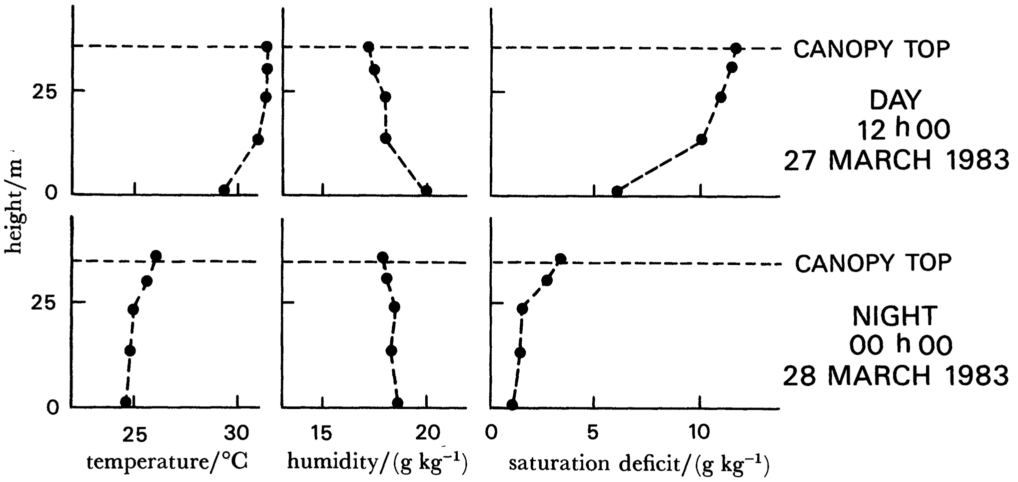

FIGURE 7. Average air temperature, atmospheric specific humidity and water-vapour saturation deficit as a function of height measured through the canopy of a tropical rain forest near Manaus, Amazonas in the middle of the day and the middle of the night. (Redrafted from Shuttleworth *et al.* (1985).)

Figure 7 suggests that the mechanisms responsible for the enhanced transfer of energy flux immediately above both temperate and tropical canopies, reported in §5*a*, do not necessarily require a distinct, elevated foliage concentration. They may be associated with enhanced wind speed at some level in the canopy, but present data for tropical forests are not definitive in this (see figure 5).

6. INTERCEPTION OF PRECIPITATION

The fact that high-latitude temperate forest canopies intercept and retain snow is an important hydrological difference between tropical and temperate forest that is outside the terms of reference of this paper. Tropical forests do not experience freezing temperatures and it is only for rainfall interception that direct comparison can be made.

In principle the fractional interception loss of forest vegetation is a simple measurement, and there is much literature for both tropical and temperate forests. In practice these data are of limited use unless indexed to a model because the value of net loss is strongly linked to ambient weather and is very variable (Dolman 1987; Shuttleworth 1988). It is in the context of such a model that the comparison is made in §6*b*.

The operational environment of the two forest biomes is sufficiently distinct that there is a difference in the reliability of experimental systems normally used to measure rainfall interception. This difference has impact on the credibility of results, particularly those from tropical forests, and is discussed first.

6a. *Rainfall interception measurement*

The primary problem in measuring the rain intercepted by a forest canopy is to determine the amount of rain reaching the ground. There is always a significant sampling error and two approaches are used to minimize this. The first is to use multiple rain gauges to measure drip from the canopy and the flow down the trunks. Many studies have located these in fixed positions, but a better experiment will regularly relocate throughfall gauges at randomly chosen positions beneath the canopy to reduce sampling errors. Often relocation is made between discrete positions in a rectangular grid or along a linear transect to improve efficiency (see, for example, Gash *et al.* 1980). The second approach is to erect a very large rain gauge, often made out of plastic sheeting (Calder & Rosier 1976). This is sealed to the trunks of any enclosed trees and is typically a square of 10 m side. Water entering this rain gauge is ducted to a measuring system the capacity of which must be commensurate with the area sampled.

Both these techniques have been successfully used in temperate forests and both have been applied in tropical forests, although their performance is then more problematical. Lloyd & Marques (1988) provide evidence of a significant difference in the statistics of throughfall drip, which is arguably characteristic of mature temperate and tropical canopies. This is illustrated in figure 8*a*, *b*, which shows the probability distribution of the throughfall fraction for individual storms. Tropical forests have a much broader distribution with evidence of concentration in widely spaced, and therefore only occasionally sampled, drip points, and consequently enhanced depletion elsewhere.

These data can be used (Lloyd & Marques 1988) to assess the likely quasi-random errors according to the number of gauges used and random relocations made. Figure 8*c* illustrates the case of tropical forests for the probability distribution in figure 8*a*. The asymptotic limit of the error shown is that imposed by a finite number of sample points in the discrete grid used for probability sampling. The use of a limited number of fixed gauges is shown to be particularly prone to considerable sampling error. Many studies of interception have used such a sampling strategy for tropical forests (see, for example, Franken *et al.* (1982)), and this has presumably contributed to the extreme variability in interception fraction reported in reviews of tropical interception (see, for example, Clarke 1988). More importantly, any predisposition by past observers to discard apparently unrealistically high measurements among their data, or to move individual gauges away from apparently unrepresentative drip points in a fixed sample position measurement, would generate a significant systematic error, tending to overestimate interception loss.

Lloyd *et al.* (1988) also report the use of the large plastic-sheet rain gauge (Calder & Rosier 1976) in the tropical environment. Ultimately data from this system were considered unreliable and discarded. This was partly because of frequent leaks in the plastic sheet, but also because the water collection and gauging systems were not considered adequate for the rainfall intensity of tropical storms. Inadequate gauging gives an underestimate in the measured throughfall, additional to that resulting from gauge leakage, and a (fractionally enhanced) overestimate in the interception loss, because this is calculated as difference between large terms. The loss, moreover, increases with progressively heavier storms. If not recognized, this

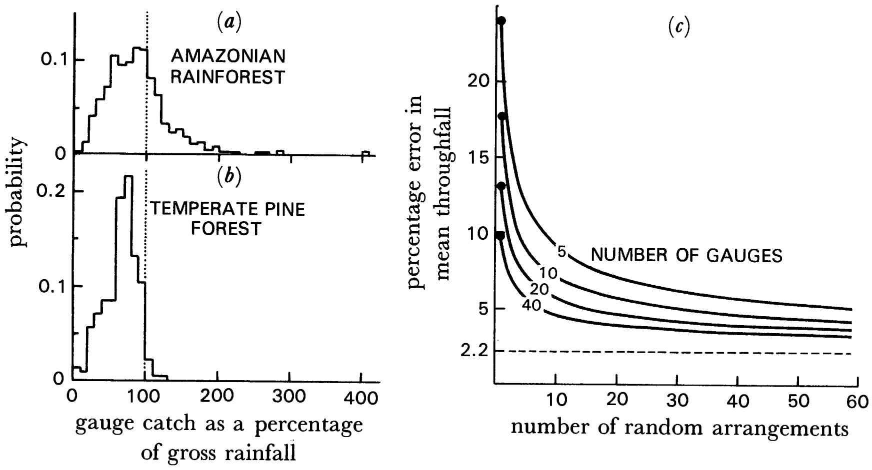

Figure 8. (*a*) Probability of fractional throughfall catch measured for individual storms with randomly relocated rain gauges beneath the canopy of an Amazonian rain forest near Manaus, Brazil; (*b*) as (*a*), but measurements made beneath a temperate Scots pine forest near Thetford, England; (*c*) percentage error in average measured throughfall calculated from the probability distribution shown in (*a*) for different numbers of rain gauges and increasing numbers of random rearrangements. (Redrafted from Lloyd & Marques (1988).)

may be misinterpreted as the consequence of a large canopy interception store, the value of which is asymptotically approached with increasing storm size (Calder *et al.* 1986).

6*b*. *Rainfall interception model*

The simplest model of interception is to treat the whole canopy as a single moisture store, which is filled by incoming rainfall and drains at a rate expressed as an empirical function of its proportional fill. Some proportion of the rain falls straight through. Water leaves the canopy either as throughfall (drip) to the ground, or runs down the trunks of the trees. A subsidiary loss may arise as a result of evaporation from the wet trunks and some workers (for example, Rutter *et al.* (1971)) estimate this from a submodel whose mathematical behaviour mimics that of the canopy. The rate of evaporation from the interception stores is usually assumed equal to that given by the Penman equation for a totally wet canopy (Monteith 1965), scaled down by the proportional fill if the store is partly empty. This last assumption seems adequate within the limited experimental evidence available (Shuttleworth 1978), and is in any case not critical to the calculation of integrated interception loss.

The model just outlined is that proposed by Rutter *et al.* (1971), but researchers have sometimes modified this to improve the description of their own experimental data. Some have implemented the same principles in a multilayer description (see, for example, Sellers & Lockwood (1981)), others have used different empirical drainage functions (see, for example, Calder 1977; Massman 1980, 1983), or modified the assumed approach to canopy saturation (Aston 1979; Calder 1986). Clearly such qualification has value in providing a better description of site-specific measurements, but it is not obvious that it significantly improves the likely accuracy of truly predictive application, when more fundamental parameters, in particular canopy storage, S, aerodynamic resistance, r_a, and the proportion of rain falling straight through the canopy, p, must be assigned without reference to experimental data.

Because the fraction of rain intercepted is so variable, but the conceptually simple model

Table 1. Canopy Store, S, free throughfall fraction, p, and aerodynamic resistance formulation for models of rainfall interception, conceptually of the Rutter *et al.* (1971) form, for temperate and tropical forest stands

stand	canopy store, S/mm	free throughfall fraction, p	aerodynamic resistance	source of data (comments)
temperate coniferous				
Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melville)	1.05	0.25	standard[a]	Rutter *et al.* (1971)
Scots pine (*Pinus sylvestris* L.)	0.80	0.26	standard[a]	Gash & Morton (1978)
	1.02	0.13	standard[a]	Gash *et al.* (1980)
Monterey pine (*Pinus radiata* (D. Don))	1.04	—	—	Aston (1979)[c]
Norway spruce (*Picea abies* (L.) Karst.)	1.50	0.25	standard[a]	Rutter *et al.* (1975)
Sitka spruce (*Picea sitchensis* (Beng.) Carr.)	1.73	0.05	fixed at 3.5 s m^{-1}	Calder (1977)[b]
	2.50	—	—	Hancock & Crowther (1979)[e]
	1.20	set to zero	standard[a]	Gash *et al.* (1980)
	0.75	set to zero	standard[a]	Gash *et al.* (1980)
Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)	1.20	0.09	standard[a]	Rutter *et al.* (1975)
	1.50	0.05	—	Massman (1983)
temperate (other)				
oak leafy (*Quercus robur* L.)	0.88	0.45	standard[a]	Thompson (1972)
oak leafless (*Quercus robur* L.)	0.28	0.80	standard[a]	Thompson (1972)
oak summer (*Quercus robur* L.)	0.80	0.30	standard[a]	Dolman (1987)
oak winter (*Quercus robur* L.)	0.30	0.80	standard[a]	Dolman (1987)
Eucalyptus sp. (6 species)	0.20–0.80	—	—	Aston (1979)[c]
Acacia longifolia (Andrews) Willd.	0.60	—	—	Aston (1979)[c]
tropical				
mixed species (Indonesia)	1.10	set to zero	fixed at 0.5 s m^{-1}	Calder *et al.* (1986)[b] (optimum values, but data inconsistent with Rutter model)
	4.90	set to zero	fixed at 5.0 s m^{-1}	(optimum values with 'stochastic' formulation of canopy storage, following Calder (1986))
mixed species (South America)	0.74	0.08	standard[a]	Lloyd *et al.* (1988)

[a] A standard description of aerodynamic resistance, in this context, implies the conventional wind speed dependent formula relevant in neutral conditions (see equation (6)) with d and z_0 expressed as a fraction of forest height.

[b] Data collected with a large plastic sheet train gauge (see Calder & Rosier (1977) and §6*a*).

[c] Using tree weighing and artificial rain.

[d] Using gamma ray attenuation.

[e] Using branch weighing.

described above so commonly provides an adequate description (with one exception described later), it is in terms of the basic parameters of this model (S, r_a and p) that the comparison between temperate and tropical forests is made. Table 1 presents values of these parameters for temperate and tropical forest sites where a Rutter-type model was actually used or, in effect, assumed.

In most cases when using these models, the formula for aerodynamic resistance used, and found satisfactory, was that relevant to the transfer of momentum in thermally neutral atmospheric conditions, i.e.

$$r_a = 1/k^2u\,[\ln{(z-d)/z_0}]^2, \tag{6}$$

but some authors found an adequate, or even slightly improved, model description when r_a was set to a constant value (see, for example, Calder 1977). Both S and p vary greatly in table 1, even when attention is limited to coniferous forests in temperate zones, where most work has been done.

The value of p is important only when it starts to rain or during low-intensity storms, when the rainfall rate may not be sufficient to support evaporation otherwise limited by energy availability. Sensitivity analyses in temperate coniferous forests (see Gash & Morton 1978) and tropical forests (see Shuttleworth 1988) suggest that with $S \approx 1$ mm, large (50%) changes in p give only a few percent change in the calculated interception loss. In many cases assigning an arbitrary value, say $p = 0.1$, would allow adequate simulation of field data within likely experimental error. Temperate deciduous forest is different. On the basis of the limited data available, p is larger (approximately 0.4) when the forest is in full leaf, and larger still (approximately 0.8) when there are no leaves present.

The mean and standard deviation of all the values of S given in table 1 for coniferous forest is 1.4 ± 0.5 mm. For unknown reasons the values deduced other than from modelling studies seem, in general, to be systematically larger and neglecting these reduces the average to 1.2 ± 0.3 mm. On the basis of present evidence, S is rather less for deciduous forests, (say) 0.8 mm when they are in leaf and 0.3 mm when they are leafless. Gash & Morton (1978) estimate that a 50% change in S produces a 15% change in total interception for a temperate coniferous forest, whereas Shuttleworth (1988) estimates that the same change in S produces a 25% change in total interception for a tropical forest. This difference is plausible bearing in mind the relative intensity and duration of storms and the likely change in the proportion of evaporation arising from after-storm canopy drying. Using the sensitivity given above, a 25% change in the value of S ($= 1.2$ mm) for coniferous forest is estimated to generate only a 7% change in the intercepted precipitation.

There is currently an important but unresolved inconsistency in the literature regarding the interception process for tropical forests. Lloyd *et al.* (1988), working in the Amazon basin, showed that the Rutter model and its analytical equivalent (Gash 1979) both provide an adequate description of data gathered using the randomly relocated rain gauges in a measuring grid system. They reported a canopy store of 0.74 mm, a free throughfall fraction of 0.08 and assume standard form for the aerodynamic resistance (i.e. eqn 6). The slightly high model estimate, about 12% compared with a measured value of 8.9 ± 3.6%, was considered to result from enhanced (rainfall-rate dependent) drainage, which was not included in the model. They discarded data simultaneously collected with a large, plastic sheet rain gauge, on the grounds that it was prone to overestimate interception loss in that tropical environment. Calder *et al.* (1986), on the other hand, reported data gathered by similar plastic sheet rain gauges in an

Indonesian rain forest. They found that their measured interception loss, approximately 20%, cannot be described by a Rutter model in which, even with (unrealistic) optimized parameters, estimates were too low by about a factor of two. They were, however, able to provide an adequate description with a canopy storage that is implicitly related to storm size and effectively much larger.

This inconsistency is very significant. If the result of Calder *et al.* (1986) is not attributable to experimental method, as seems probable (see §6*a*), new and more complex models of interception are required in general, and for tropical forests in particular. Equally, the Lloyd *et al.* (1988) data must be low, by about a factor two, for unexplained reasons, although this is unlikely because it would probably also imply persistent energy advection to Amazonia at the continental scale. Clearly this aspect of the micrometeorology of tropical forests merits further attention to resolve the inconsistency.

7. Stomatal control

If there is no rain or dew on the vegetation, water loss from a forest with a full canopy occurs through stomata in the foliage, via trunks, stems and branches from the soil. When energy is readily available, water-vapour flow is restricted to maintain an approximate balance with the water available, within the plant's ability to define this. Ultimately the difficulty in extracting water from the soil intervenes to close stomata possibly via a chemical regulator; but the stomata – soil moisture interrelation is initially weak and ultimately nonlinear (see, for instance, Rutter (1975)), and the control is more subtle than this. Genetics and environmental conditioning of plants provide foliage with a stomatal response that changes with the local micrometeorological environment. The response, having common purpose, is often qualitatively similar from one species to the next, but none the less exhibits marked variation in quantitative terms.

Trees in forests are typical of all plants in this respect. In field conditions forest vegetation rarely functions without one or more aspects of the environment acting to reduce stomatal opening from its maximum. Laboratory experiments with small plants or individual shoots can show the response to separate environmental variables. The variability in stomatal behaviour can be startlingly large, even between ostensibly similar species. Jarvis *et al.* (1976), for instance, reported the value of minimum (unstressed) stomatal resistance for 16 species of temperate, coniferous needles: the values vary by a factor of 20. Some of this may be the result of inconsistency or inadequacy in experimental method, but species, age and site also contribute differences. A factor of at least two in the magnitude of the numerical parameters describing the stomatal resistance of individual leaves and its response to environment is common to both temperate (see, for example, Jarvis *et al.* 1976; Rutter 1975) and tropical forest trees (see, for example, Chiariello 1984). Comparison in this regard has little value: a growing literature merely suggests that they are consistent within a (possibly biased) sample of the large species variability in each biome.

Numerical disparity in stomatal response between individual species is less relevant when describing the whole-canopy interaction. Canopy average stomatal resistance is related (see Shuttleworth 1976*a*, 1978, 1979) to the so-called surface resistance, r_s, of the stand defined by Monteith (1965). The variability in r_s between forest stands in similar day-time conditions is less than that observed in the individual relations at stomatal level (see §7*b*).

It is perhaps reasonable that selective pressure should achieve a better definition of average whole-canopy behaviour than it does of the minimum stomatal resistance, or of the functions describing the stress to individual variables. Stress factors can act in unison to produce the same value of r_s in different ways, given the natural variability of near-surface weather parameters. Forests have a midday value of r_s typically larger than that of other vegetation, (say) 100 ± 30 s m^{-1} (see § 7*b*) and often exhibit a marked response to water-vapour saturation deficit (see §7*a*). This may reflect their characteristic tall and perennial nature: the evaporating foliage is more remote from moisture in the soil and, presumably, more vulnerable to falls in leaf water content in the daily cycle of evaporative demand. Such demand is, in turn, more directly related to water-saturation deficit than for other kinds of vegetation classes, because of the enhanced turbulent interaction (see §5). Higher values of r_s and an increased response to atmospheric water-vapour deficit are, perhaps, thus a necessary and characteristic feature of forests.

7*a*. *Response to the environment*

The immediate cause of change in stomatal pore size is change in water content and turgor of the associated guard cells, but the effect and interaction of external variables on guard-cell movement is complex and poorly understood. Rutter (1975) suggested that (local) CO_2 concentration is an important aspect of guard cell response but, according to Jarvis (1980), the main variables controlling the stomata of temperate conifer forest are photon flux density, needle temperature, water-vapour saturation deficit of the air and needle (leaf) water potential, with little observed response to CO_2 concentration (Jarvis *et al.* 1976). Direct studies of the stomatal resistance for tropical tree species (see, for example, Chiariello 1984; Pearcy 1987; Roberts *et al.* 1989) demonstrate broadly similar behaviour to that observed in temperate coniferous forest, particularly for sensitivity to light and saturation deficit.

The demand for a working description of whole-canopy surface resistance is such that empirical formulae are proposed for forest and calibrated against micrometeorological data. Usually the general form of the stomatal responses to environmental variables observed for individual leaves is transposed to describe the whole-canopy (see, for example, Stewart 1988; Gash *et al.* 1988). It is instructive to compare the results of calibrating similar assumed forms for the surface conductance, the reciprocal of surface resistance, for temperate and tropical forest stands. Three significant calibrations have been reported for temperate coniferous forest (Lindroth 1984; Stewart 1988; Gash *et al.* 1988) and one for natural Amazonian rainforest (Sellers *et al.* 1989). In fact this last calibration is within a complex computer model in which the implicit description of surface conductance is difficult to identify and interpret. An appendix to the present paper corrects this: an explicit expression for the surface conductance of tropical forest is defined with comparable form to those for the temperate forest stands.

The basis of the present comparison is an expression for whole-canopy surface conductance, g_s, which is assumed to take the parametric form

$$g_s = g_0 g_C g_R g_D g_T g_M, \tag{7}$$

where g_0 is a value characteristic of the forest, corresponding to the unstressed value at a specified leaf-area index, green-leaf fraction and leaf age, and an incident solar radiation of 1000 W m^{-2}; g_C is a canopy cover function, representing the combined effect of seasonal changes in leaf-area index, green-leaf fraction and foliage ageing: g_R is a radiation stress function, which is set to unity for an incident solar radiation of 1000 W m^{-2}; g_D is an atmospheric water-vapour saturation deficit stress function, which is unity for a saturated atmosphere; g_T is a temperature stress function, which is unity at a specified optimum needle temperature and falls either side of this; and g_M is a soil moisture status stress function, which is unity when the soil is saturated through the rooting zone. Particular forms are assigned to these functions by individual investigators but it is convenient here to specify common parametric forms for g_R and g_T as follows:

$$g_R(S_R) = [S_R(1000+K_R)]/[1000(S_R+K_R)] \tag{8}$$

and

$$g_T(T) = [(T-T_L)(T_H-T)^a]/(T_o-T_L)(T_H-T_o)^a, \tag{9}$$

where

$$a = (T_H-T_o)/(T_o-T_L) \tag{10}$$

and S_R is the incident solar radiation, in watts per square metre, T is the (surface) temperature of the vegetation, in kelvins, and K_R, T_H, T_L and T_o are constants characteristic of the forest stand.

In two of the temperate forest calibrations (Stewart 1988; Gash *et al.* 1988) g_D is specified as

$$g_D(D) = 1-K_D D \quad (\text{for } D < D_C) \tag{11}$$

$$= 1-K_D D_C \quad (\text{for } D \geqslant D_C) \tag{12}$$

where D is water-vapour saturation deficit and D_C and K_D are characteristic constants.

For the third coniferous forest (Lindroth 1984) a different form was assumed thus

$$g_D(D) = (1-D/K_D^0)^{-1}. \tag{13}$$

For the tropical-forest calibration the (effective) parametrization for g_D, which is derived in the Appendix 1, has the form

$$g_D(D) = 1-K_D^1 D+K_D^2 D^2. \tag{14}$$

The constants K_D, K_D^0, K_D^1 and K_D^2 in equations (11–14) are here linked to values of water-vapour saturation deficit, (D), and limiting value, D_C, both expressed in units of grams per kilogram. It is shown later that with particular values of forest-specific constants these three equations have broadly similar form.

Two of the temperate forest calibrations (Stewart 1988; Gash *et al.* 1988) quote optimized values of g_o under the assumption that g_s is directly related to leaf-area index, with g_o corresponding to the maximum value of leaf area in a particular seasonal pattern measured by Beadle *et al.* (1982) . In these two cases g_C is then assumed to be the normalized value of this prescribed annual variation in leaf-area index. Although g_s is expected to show some response to increasing leaf area, a direct relation between the two is unlikely, see for instance Sellers (1985, figure 15). In practice, additional leaves are exposed to significantly less light and make a proportionately reduced contribution to the whole-canopy conductance and vice versa. (Note. Surface conductance is still, to first order, the product of leaf area with mean stomatal conductance (Monteith 1965), but the mean stomatal conductance is less.) In fact, g_C is a complex convolution of a more moderate response to leaf area with other seasonal factors such as leaf age and canopy greenness, these being expressed relative to the appropriate values at calibration. The form of this function is not defined for the four calibration forests described here, although it may ultimately prove amenable to remote-sensing measurement (Sellers *et al.* 1989). Pending this, it is preferable to set g_C to unity for these evergreen forests, and quote a value of g_o appropriate to the annual average value of those variables that determine g_C, and in particular that of leaf-area index. The values of g_o given here have therefore both been adjusted down by a factor 0.76 from those reported by Stewart (1988) and Gash *et al.* (1988), this being the ratio of the average leaf area to the peak leaf area in their assumed seasonal variation. This is also appropriate because both these forests have an understorey the leaf area of which is not recognized in the leaf-area function.

The form of the soil moisture stress function, g_M, has been parametrized differently, though the general form is an initially weak response, with a subsequent rapid fall (to zero) as the moisture content approaches that available in the forest's rooting zone. The limit is more related to the underlying soil than it is to the plants; it is typically 20% of soil volume but can vary from (say) 7% for sand to 30% for peat (see Rutter 1975). In only one of the four calibration studies was soil moisture reduction sufficient to allow calibration of this stress factor, and even then the limiting behaviour of the function was poorly defined. Stewart (1988) specifies a form of g_M for a pine forest (with bracken understorey) growing in sandy soils, which can be written as

$$g_M(SM_D) = 1 - K_M^1 \exp\,[K_M^2(SM_D - SM_D)], \qquad (15)$$

where SM_D is the soil moisture deficit averaged over the rooting zone, and SM_D, K_M^1 and K_M^2 are constants, with optimized values of 69.7, 0.34 and 0.081, respectively. The optimum value of SM_D determined for this site is consistent with a water availability of about 7% of soil volume, assuming an effective rooting depth of about 1 m in a sandy soil. Sellers *et al.* (1989) assumed an expression for g_M for Amazonian rainforest (see Appendix 1) but this, like equation (15), remains uncalibrated for the Amazon site.

Table 2 gives the optimized values of the constants defining surface conductances as deduced by calibrating equation (7) against micrometeorological data for the four calibration forests. In the Jädraås forest calibration g_T and g_M were set to unity and equivalent parameters are not therefore defined in table 2: because these are usually close to unity this assumption is unlikely to alter the optimized values of K_R or K_D^0 greatly, but may reduce the optimized value of g_o. Figure 9 illustrates the ensuing form of g_R, g_T and g_D. There is evident similarity in the size and environmental dependence of the surface conductance for these four forests. The value

TABLE 2. VALUES OF THE CALIBRATION CONSTANTS IN EQUATION (7), AND ASSOCIATED EQUATIONS WHICH SPECIFY THE CANOPY CONDUCTANCE OF TWO TEMPERATE AND ONE TROPICAL FOREST STANDS

(Missing values imply no equivalent calibration was made or possible. The value of g_c is set to unity pending the specification of a suitable seasonal function related to the leaf-area index, green-canopy fraction and foliage age. (The value of g_0 for Jädraås forest is likely to be lower by 5–10% than it would be with a joint optimization including g_T and g_M.))

parameter	equation	Thetford (Stewart 1988)	Les Landes (Gash *et al.* 1988)	Jädraås (Lindroth 1984)	Amazon (see Appendix 1)
$g_0/(\mathrm{mm\ s^{-1}})$	7	17.9	24.2	20.3	22.9
g_C	7	1	1	1	1
$K_R/(\mathrm{W\ m^{-2}})$	8	104	256	137	248
T_H/K	9, 10	313	313	—	318
T_L/K	9, 10	273	273	—	273
T_o/K	9, 10	291	293	—	303
$K_D/(\mathrm{g\ kg^{-1}})^{-1}$	11, 12	0.081	0.061	—	—
$D_C/(\mathrm{g\ kg^{-1}})$	11, 12	9.44	10.88	—	—
$K_D^0/(\mathrm{g\ kg^{-1}})$	13	—	—	5.63	—
$K_D^1/(\mathrm{g\ kg^{-1}})^{-1}$	14	—	—	—	0.055
$K_D^2/(\mathrm{g\ kg^{-1}})^{-2}$	14	—	—	—	0.00054
K_M^1	15	0.34	—	—	—
$K_{SM}^2/(\mathrm{mm})^{-1}$	15	0.081	—	—	—
SM_D	15	69.7	—	—	—

of g_0 for Les Landes and Amazon forest agree within ±3%, whereas Jädraås and Thetford are 14% and 24% less, respectively. The value of g_0 for Jädraås is expected to be (say) 10% lower to compensate for the absence of the g_T and g_M factors during optimization. The lower value for Thetford may, in part, be associated with physiological changes during the (U.K.) drought years of 1975 and 1976 when most of the calibration data were collected: there is some evidence for this in the calibration (see Stewart 1988). This forest does, however, seem to have a systematically lower value of surface conductance than other coniferous stands even in more typical years (see §7*b*), possibly related to its low planting density and leaf area index.

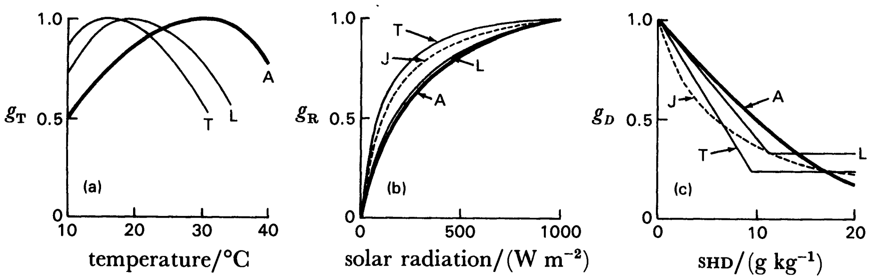

FIGURE 9. Normalized stress factors acting on the whole-canopy surface resistance for four forest canopies (see equation (7) corresponding to (*a*) temperature, (*b*) solar radiation and (*c*) atmospheric specific humidity saturation deficit. The curves are indexed as follows: A, Amazonian rain forest (Manaus, Brazil); L, maritime pine (Les Landes, France); T, Scots–Corsican pine (Thetford, England); J, Scots pine (Jädraås, Sweden).

The similarity in stress factors shown in figure 9 is also satisfactory. The three forests for which g_T is defined seem to be adapted to different optimum temperatures (see figure 9*a*) but this is to be expected, and the optimum values change in a plausible way with latitude (and climatological average temperature). The agreement between Les Landes and the Amazon forests in the functional form of g_R and g_D is again good, see figure 9*b*, *c*, but it is significant that these functions act in opposite senses. There is a statistical correlation between higher radiation and higher saturation deficit at both the daily and seasonal timescales, and this will produce some net cancellation between these stress factors acting in unison in equation (7). It is, of course, possible that the (complementary) differences in g_R and g_D reported for these four forests are merely a statistical artefact of their (joint) optimization during calibration. It is more interesting to speculate that the forests are themselves responsible. The two higher latitude forests, where light is in shorter supply, certainly have greater sensitivity to radiation but they have a complementary enhanced response to saturation deficit. Perhaps this is to maintain the surface resistance at a level appropriate to the ability of the root system of the forests to scavenge water from the soil. Thetford forest was artificially planted on a poor, free-draining, sandy soil: it has difficulty maintaining sufficient root growth to compensate for lower average soil water availability, resulting in a lower value of g_0.

7*b*. *Daily trends*

Figure 10 shows reported trends in g_S for several temperate coniferous forests, one temperate deciduous forest and one tropical forest. The separate curves represent very different amounts of data. Five of the curves (for four forests), namely Amazon (Shuttleworth 1988), Les Landes (Gash *et al.* 1988), Jädraås (Lindroth 1984) and Thetford (Stewart 1988; Gash & Stewart 1977), are average values over at least one field season, the last being a smoothed average.

These five curves are plotted as full lines, with the tropical forest drawn as the heavier line. Examples of other data for temperate forest are presented for single days and are drawn as broken lines: these data are taken from Jarvis *et al.* (1976: University of British Columbia (UBC), Canada; Fetteresso, Scotland) and Milne (1979: Rivox, Scotland). The heavy broken line is the median from six days of measurements for a temperate deciduous forest from Verma *et al.* (1986: Oak Ridge, U.S.A.), after omitting values early in the day known to be affected by heavy dew and overnight rain.

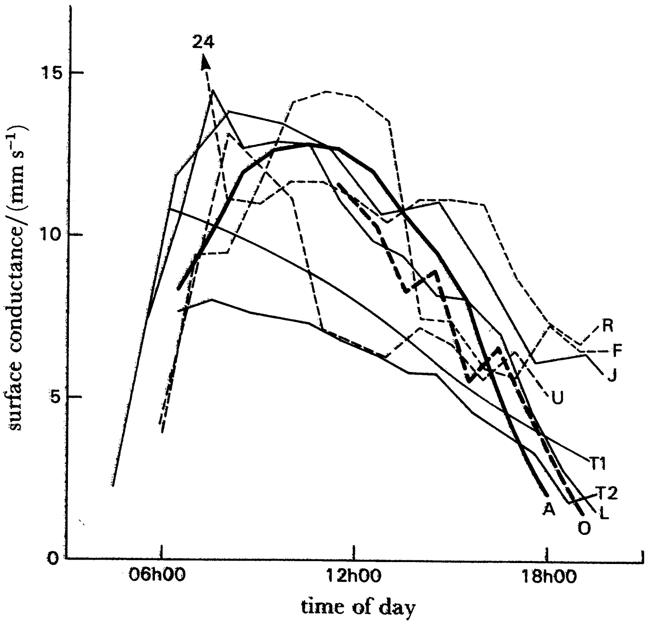

FIGURE 10. Daily variation in whole-canopy surface conductance for eight forest canopies. The curves are indexed as follows; A, Amazonian rain forest (Manaus, Brazil; three season average); F, Sitka spruce (Fetteresso, Scotland; one day); J, Scots pine (Jädraås, Sweden, season average); L, maritime pine (Les Landes, France: season average); O, oak–hickory (Oak Ridge, U.S.A.; six-day average); R, Sitka spruce (Rivox, Scotland; one day); T1, Scots–Corsican pine (Thetford, England; seasonal average, typical season); T2, Scots–Corsican pine (Thetford, England; seasonal average, drought season); U, Douglas-fir (Research Forest, Canada; one day).

Because the data in figure 10 come from forests at different latitude, day-length variation occurs between sites. In fact, the mean daily trend for Jädraås reported by Lindroth (1984) was normalized with day length, and figure 10 arbitrarily assigns a 16 h day for plottings. Three of the curves that are long term averages (Amazon, Les Landes and Jadraas) agree well, but that for Thetford is systematically lower, by about 30% in a typical year (curve T1, Gash & Stewart (1977)) and lower still in a drought year (curve T2, derived from Stewart (1988)). The three single day samples (Fetteresso, Rivox and UBC) have a broadly similar trend to the other sites though there is, of course, greater hour-to-hour and site-to-site variation. Dew contamination is probably responsible for the unexpectedly high early morning values reported for Fetteresso. The data for temperate deciduous forest, although limited, show satisfactory similarity with the other forests.

On the basis of figure 10, a suitable day-time average value of surface conductance for forests is 10 mm s^{-1} ($r_s = 100$ s m^{-1}). It is important to point out that this is not the value that is relevant in any attempt to apply the Penman–Monteith equation by using mean daily values of the meteorological variables (see, for instance, Thom & Oliver (1977)) and Gash (1978). The calculation given by this equation is one of rate: evaporation, which in reality largely occurs during the day, is implicitly assumed to occur more slowly over 24 h in such a calculation, and the effective value of r_s is increased by almost a factor two (Shuttleworth *et al.* 1984*a*).

8. Summary and discussion

A simple model that visualizes the whole canopy acting as an entity provides a robust, time invariant representation of micrometeorological interaction, and is here the primary basis of the comparison between temperate and tropical forests. Between the two forests biomes there are differences that are mainly a matter of degree: tropical forests tend to have larger species content, height and biomass, and additional foliage more uniformly distributed in the vertical. However, they share the forest characteristics most important to their micrometeorology, namely they are extensive, dense, tall and perennial.

The fact that forests are dense is important, because it means that mass and energy conservation, applied as a spatial average, are more directly felt by individual trees; and that incoming fluxes from the atmosphere interact initially with the tree canopy. Well-separated trees may well have (indirect) access to energy and water from an area larger than they subtend, and some incoming entities can reach the ground with little intervention by the trees. A forest's extensive nature is also important, because it means that the more important aspects of the micrometeorological interaction can be represented in one (vertical) dimension. This does not mean there is no horizontal movement in the atmosphere above or soil beneath, merely that there is little need to consider horizontal movement in the canopy itself.

To say the tallness of trees is important to their micrometeorological interaction is to oversimplify. Some of the important aspects are more directly related to the overall scale of forest vegetation, rather than its height. The characteristically high efficiency of radiation and momentum capture (see §§4 and 5) is more directly a function of the relative depth to separation of depressions in the canopy top. Other shorter vegetation (e.g. heather) or mixed species with non-uniform canopy cover can mimic this to some extent. The link to height is more a statistical one: increased canopy height is linked with an increased loss in absolute precision in defining that height, and an increased separation between component plants.

Regardless of the mechanisms responsible, the solar reflection coefficients for temperate and tropical forests are both about 0.12 near midday, although there is a marked stand-to-stand variability of about ±0.03 for temperate coniferous forest (see §4*a*). Present evidence suggests deciduous forests, when in leaf, have a reflection coefficient about 0.02 greater than this. In both cases most of the radiant energy is intercepted before reaching the ground (see §4*b*) although some temperate tree canopies are sufficiently sparse to allow an understorey of distinct species, which intervenes during the summer months to exploit the radiation transmitted through the canopy.

All forests are efficient at absorbing momentum from the atmosphere, and the overall scale of the vegetation is again responsible. The tallness of forests also makes the consequences of K-theory failure just above and within vegetation more amenable to field observation (see §5*b*), because it sets the scale over which experiments can be made. The observable consequences of such failure seem to be the same just above dense temperate and tropical forest (see §5*b*), but the in-canopy consequences are less obvious in tropical stands because the foliage is more uniform with height. Fortunately, in neither case is this theoretical difficulty of serious consequence when modelling the energy partition of the forests (see §5*a*).

The specification of aerodynamic roughness therefore remains relevant, and is indeed an important distinguishing characteristic of forest vegetation. The roughness length, z_0, and zero-plane displacement height, *d*, are very variable from one forest stand to the next, varying, like albedo, with tree density; but on the basis of present evidence z_0 and *d*, expressed as a fraction of tree height, *h*, are about $0.08h$ and $0.8h$ for temperate coniferous forests, and $0.06h$ and $0.86h$ for tropical stands (see §5). The value of *d* is a larger proportion of *h* than for agricultural crops, and z_0 correspondingly less: this mainly reflects their perennial nature and an ensuing tendency towards relatively high foliage on new growth. The difference between temperate and (unmanaged) tropical stands is an extension of this argument.

It is the indirect effect of vegetation height, acting through enhanced turbulent transfer, that gives forests their distinctive difference in evaporative behaviour, depending on whether they have a wet or a dry canopy (see, for instance, Shuttleworth & Calder (1979)). Wet vegetation can evaporate freely during and immediately after rainfall, often seeking energy from the atmosphere to support the increased evaporation. Simple single level, fixed value, canopy storage models of interception (see, for example, Rutter *et al.* 1971) have been successfully used to describe this process in temperate forests, with a store that varies from one forest to the next but is about 1.2 ± 0.3 mm (see §6*b*). Usually, a simple, conventional expression for aerodynamic resistance is adequate (see equation (6)), and these models are fairly insensitive to the proportion (typically 10%) of the rain assumed to fall directly through the canopy (see §6*b*). The same modelling approach has been used successfully with temperate deciduous forests, but in this case the store is rather less, (say) 0.8 mm in full leaf and 0.3 mm when leafless, and the proportions of rain falling directly through are larger, typically 40% and 80% at corresponding times of year.

The adequacy of this same model in describing the rainfall interception for tropical forests is in some dispute (see §6*b*). One careful experiment (Lloyd & Marques 1988; Lloyd *et al.* 1988) has thrown doubt on a great deal of earlier data collected in this biome both with fixed position through-fall gauges and with large plastic sheet gauges see (§6*a*). This experiment validates the use of the same models as with temperate forests, but suggests a canopy storage of just 0.75 mm (see §6*b*). It is suggested that the combined effect of adaptation towards rain-shedding leaf characteristics and the dislodgement of already captured drops in the subsequent (heavy) rain are responsible for this reduction. However, a second experiment (Calder *et al.* 1986), with large plastic sheet gauges, gives the opposite result and suggests the need for a model with an increased, rain-rate-dependent store in tropical environments. It is not yet clear whether this is the case, or merely a consequence of shortcomings in experimental method.

The perennial nature of forests means that there is an association between the need to preserve the species and individual plant survival. Perhaps this and taller plants (with associated difficulty in relating transpiration demand in the foliage to supply from the roots) are responsible for a defensive approach to water conservation. Certainly forests in both temperate and tropical climates tend to have a somewhat higher whole-canopy surface resistance than other crops, perhaps to compensate for their lower aerodynamic resistance. They also have a marked compensatory response to atmospheric saturation deficit which, for forests, is the main control on transpiration demand. In the course of the review of stomatal control given in §7, there emerges a new and possibly important recognition of the similarity between the whole-canopy surface resistance for forests in general, and temperate and tropical stands in particular, both in terms of typical magnitude and the response to environmental variables. Clearly this is still a poorly sampled observation.

At a more practical level, it is interesting that the simplification (given in Appendix 1) of the whole-canopy stomatal response implicit in a complex computer model, involving a through-canopy integration of light dependence and causal representation of leaf water potential, results in stress factors similar to those used as an empirical description of field data for other forests. This says much about the realism and generality of the computer model on the one hand, and the adequacy of the simple empirical formulation on the other.

The very apparent general similarity between forests does not imply that they necessarily yield similar average energy partition. The same model of the micrometeorology of a forest will yield a different result depending on the meteorology to which it is exposed. This point is reinforced in figure 11, which shows a comparison between evaporation for two forests with broadly similar micrometeorological characteristics: one near the edge of a continent (a site in Wales) (Shuttleworth & Calder 1979), the second in the middle of a continent (the site at Manaus) (Shuttleworth 1988). A comparison is here made against potential evaporation rate as estimated from the Priestley–Taylor (1972) equation. The transpiration from the Welsh forest shown in figure 11*a* is very typical of many forests around the world. Forest transpiration is commonly 55–80 % of the potential rate (Shuttleworth & Calder 1979), a fact that is related to the impact of their large and effective surface resistance on a developing atmospheric boundary layer, see de Bruin & Jacobs (this symposium). The total evaporation for the two forests is larger than this: that for the Welsh forest is 30–40 % larger than the estimated potential rate (figure 11*b*); that for the Brazilian forest almost equal to the potential rate, providing that this is calculated with net radiation determined by the forest's albedo (see Shuttleworth 1988).

In the middle of a large forested continent, local radiation capture at the ground must provide energy not only for evaporation, but also as sensible heat to initiate the convection rain-generating mechanism. Forest evaporation is transpiration, which occurs at less than potential rate, with the superposition of the efficient evaporation of intercepted rainfall. This supersedes the transpiration process during and immediately after rain and commonly occurs at rates in considerable excess of the local potential evaporation rate (Shuttleworth & Calder, 1979; Shuttleworth 1988). Figure 11*b* shows that the interception process is capable of generating an average total evaporation that is significantly larger than the potential evaporation rate, but can obviously only do so when it rains. In the continental interior there must be a situation in which absorbing additional solar energy for evaporation will begin to restrict the initiation of convective rainstorms. At this point a strong negative feedback exists: figure 11*c* suggests that this is such as to define an average total evaporation rate similar to a radiation-related estimate of potential evaporation.

The implications of figure 11 and the arguments of the previous paragraph on the likely consequences of tropical deforestation are considerable. A strong energy-limit link between changes in evaporation and precipitation may help to moderate the change in river flow consequential on continental-scale deforestation. The introduction of realistic land-surface description into climate models, perhaps exploiting data of the type reviewed in this paper, will no doubt illuminate this. However, such a feedback mechanism will not necessarily be so effective near the edge of continents or in islands where many tropical forests occur (see figure 1). Here, climate is more strongly determined by the nearby ocean, less by the surface

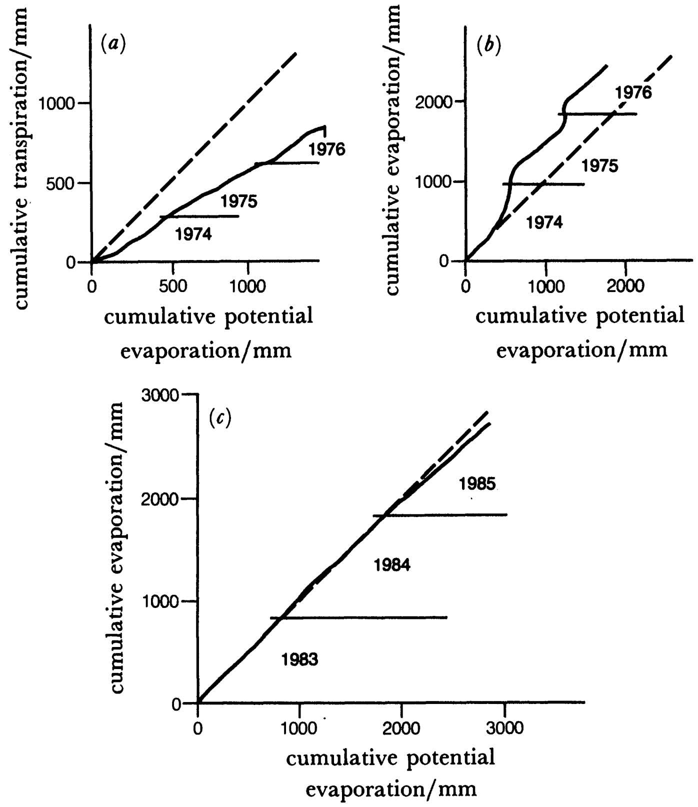

Figure 11. Comparison between forest evaporation and potential evaporation, as estimated by the Priestley–Taylor (1972) equation, for two forests, one (figures (*a*) and (*b*)) at the edge of a continent, in Wales, and one (*c*) in the middle of a continent, in the Amazon basin. (*a*) The comparison between cumulative (dry-canopy) transpiration and the simultaneous cumulative estimate of potential evaporation; (*b*) Comparison for total evaporation in both dry and wet canopy conditions. (*c*) The total monthly evaporation for Amazonian forest compared with a potential estimate based on radiation measurements relevant to the forest canopy. (Parts (*a*) and (*b*) are redrawn from Shuttleworth & Calder (1979): (*c*) is redrawn from Shuttleworth (1988).)

vegetation. Figure 11 suggests a more pronounced reduction in evaporation in this case and, assuming the precipitation remains ocean driven, presumably a more significant increase in river flow after deforestation.

The incident climate therefore changes the net energy partition, but the most consistent message of this paper is that current evidence indicates that the micrometeorological interaction of temperate and tropical forests is essentially indentical, and that most of the detail is similar. Perhaps this is not too surprising. Trees will seek to survive and propagate, and may choose disparate strategy to do so. However, the characteristic denseness and extensiveness of forest vegetation means that they are, in physical terms, a one-dimensional entity, and the conservation laws must be obeyed on an area-average basis. In doing this it is surely likely that forests will be obliged to possess common features if it is to reconcile the physical consequences of a tall growth habit with a perennial nature.

Appendix 1. The surface resistance of Amazonian rain forest

Data on Amazonian evaporation (Shuttleworth 1988) have been used by Sellers *et al.* (1989), reference hereafter called S1, to calibrate their Simple Biosphere Model (SiB), this being a land surface parametrization (lsp) specifically designed for inclusion in computer models of atmospheric general circulation (Sellers *et al.* 1986). Implicit in this calibration is a definition of the whole-canopy average stomatal control for Amazonian rain forest, but for this paper it is necessary to identify and simplify this so as to allow its comparison with similar expressions for temperate forest stands.

The formula for surface conductance, g_s $(=r_s^{-1})$, used in the SiB model can be compressed into

$$g_s = g_o\, g_R(S_R)\, g_T(T)\, g_\Psi(\Psi)\, g_D^1(D), \tag{A 1}$$

where $g_T(T)$ and $g_D^1(D)$ are defined as in equations (9) and (11) in the main text, $g_R(S_R)$ is a normalized, solar-radiation-dependent stress function, defined in detail later, and $g_\Psi(\Psi)$ and g_o are given by

$$g_\Psi(\Psi) = (\Psi - \Psi_2)/(\Psi_1 - \Psi_2) \tag{A 2}$$

and

$$g_o = V_c\, N_c\, g_{max}. \tag{A 3}$$

In equation (A 2) the variable Ψ is leaf water potential and Ψ_1 and Ψ_2 are optimized parameters, determined in S1 as -15.2 and -1553.5 m (of water), respectively. This factor (g_Ψ) is later reinterpreted as a combination of two separate stress factors, the first dependent on soil moisture tension, the second on atmospheric saturation deficit. Adopting the values given by S1, we take the fractional ground area with full canopy cover $V_c = 0.92$, the proportion of live (green) leaves in the foliage $N_c = 0.905$, and the unstressed value of g_s when the incident photosynthetically active radiation (PAR) is 500 W m^{-1}, $g_{max} = 27.5$ mm s^{-1} (see S1, figure 2*b*). Substituting these values into equation (A 3) gives $g_o = 22.9$ mm s^{-1}.

The formula for the temperature-dependent stress, $g_T(T)$, in S1 compares directly with that previously used for temperate forest (see, for example, Stewart (1988); Gash *et al.* (1988)). The constants T_H, T_L, and T_o in equations (9) and (10) for Amazonian rain forest are 318, 273 and 303 K respectively.

The expression for the light-dependent stress in the SiB model is a complex analytic integral of the convolution between an assumed form at the stomatal level and a semi-empirical description of through-canopy PAR absorption, see equations (28) and (26) of Sellers *et al.* (1989). However, the ensuing dependence is virtually identical to equation (8). It is often acceptable to estimate photosynthetically active radiation as half the flux of the incident solar radiation, S_R (see, for instance, Goudriaan (1977)). Figure a1 is redrawn from figure 2*b* of S1 with this assumption and after normalization to the value when $S_R = 1000$ W m^{-2}. Also illustrated is the expression

$$g_R(S_R) = (S_R\, 1278)/[1000(S_R + 278)]. \tag{A 4}$$

This is equation (8) with $K_R = 278$ W m^{-2}, and provides a description of the more complex formulae in SiB.

SiB includes a specific dependence on leaf water potential through g_Ψ. This implicitly includes the effect of soil moisture deficit, a factor given explicit recognition in alternative formulations of g_s (see Stewart 1988). The factor g_Ψ is also related to the flow of water through the plant and therefore to atmospheric demand which, in the case of transpiring trees, is mainly the water-vapour saturation deficit. The optimized values of Ψ_1 and Ψ_2 in equation (A 2) give

$$g_\Psi(\Psi) = 1.023 + \Psi/1518.3. \tag{A 5}$$

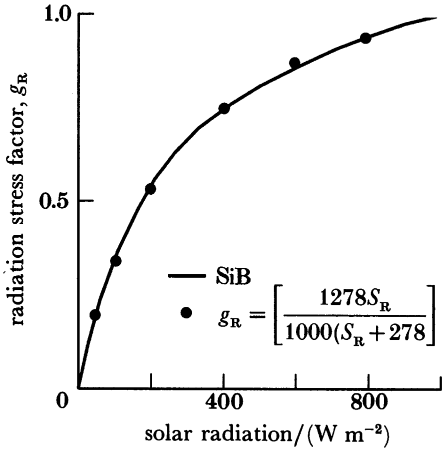

Figure a1. Comparison between the light sensitivity of whole-canopy surface conductance as synthesized within the simple biosphere model (Sellers *et al.* 1988) after calibration for the tropical forest biome (full line), and as calculated from equation (8) with $K_R = 278$ W m^{-2} (full circles). Photosynthetically active radiation is assumed equal to 50% of solar radiation in this figure.

In SiB, leaf water tension is soil water tension in the root zone, Ψ_r plus the tension necessary to raise the transpired water against gravity and resistance in the plant and soil (see equation (29) of S1), i.e.

$$\Psi = \Psi_r - z_T - E_T R, \tag{A 6}$$

where $z_T \approx 30$ m, the height of the transpiration source, E_T is the transpiration flux, and R is the combined resistance in plant and soil. In forests efficient turbulent mixing means in-canopy saturation deficit is close to that above the canopy, D, and the transpiration flux is very nearly proportional to this. Equation (A 6) can be rewritten as

$$\Psi \simeq \Psi_r - z_T - \alpha' D, \tag{A 7}$$

where α' is assumed constant to first order. Substituting equation (A 7) into (A 5) and adopting a new constant, α, gives

$$g_\Psi(\Psi_r, D) \approx 1 + (\Psi_r/1518.3) - \alpha D. \tag{A 8}$$

Results from the SiB model also suggest that g_Ψ is close to unity, typically 0.85–0.90 (see figure 13*a* of S1), and it is therefore acceptable to write equation (A 8) as

$$g_\Psi = g_M(M_F)\, g''_D(D), \tag{A 9}$$

where SM is the soil moisture fraction in the rooting zone, with

$$g_M(M_F) = 1 + (\Psi_R(M_F)/1518.3) \tag{A 10}$$

and

$$g''_D(D) = 1 - \alpha D. \tag{A 11}$$

In this way the saturation deficit stress implicit in SiB (operating in the tropical forest biome) comprises two terms. The first, g'_D in equation (A 1), is directly determined by optimization in S1 as

$$g'_D = 1 - 0.0423 D. \tag{A 12}$$

The constant is that in S1 after adjustment, because D is in grams per kilogram in this paper. The second (smaller) factor, g''_D, is not explicitly determined in S1 but can be adequately estimated. The soil moisture was always close to saturation (and $g_{\mathrm{M}} = 1$) during calibration, and the leaf water potential stress (illustrated in figure 13*c* of S1) is in fact a measure of g''_D. Careful inspection of this figure shows that g''_D and g'_D are strongly correlated, with g''_D exhibiting about 30% of the change in g'_D when it is significant in day-time conditions; hence, from equation (A 12)

$$g''_D \approx 1-0.0127D. \tag{A 13}$$

It is therefore possible to combine (A 12) and (A 13) as a single saturation deficit dependent stress factor with the form

$$g_D(D) = 1-0.055D+0.00054D^2 \tag{A 14}$$

for conditions of ample soil moisture.

In this way the calibration of the stomatal response in S1 can be rewritten in a form similar to that used to describe temperate coniferous forest and analogous to equation (7), namely

$$g_{\mathrm{s}} = 22.9\, g_{\mathrm{C}}\, g_{\mathrm{R}}\, g_D\, g_T\, g_{\mathrm{M}}(M_{\mathrm{F}}) \quad \text{(in millimetres per second).} \tag{A 15}$$

In this expression g_{R} is given by equation (A 4), g_D by equation (A 14) and g_T by equations (9) and (10). The form of g_{M} used in the SiB model for this biome remains uncalibrated because the soil was always wet, but, with the particular values of Ψ_1 and Ψ_2 from S1, this is in effect assumed to take the form

$$g_{\mathrm{M}}(M_{\mathrm{F}}) = 1-0.000\,13M_{\mathrm{F}}^{-7.8} \tag{A 16}$$

for $M_{\mathrm{F}} > 0.318$, and zero below this value (see equation (30) and table 2 of S1). Clearly, other assumed forms for g_{M}, e.g. equation (14), carry equal (uncalibrated) status. At the present time g_{C} is best set equal to unity: S1 arbitrarily prescribes constant leaf-area index and green-leaf fraction during calibration, though it is subsequently demonstrated that there is an undescribed seasonal variation in the order 5–10%. This is assumed to be associated with changes in leaf area, leaf age and green leaf fraction but the detailed dependence is not currently defined.

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Discussion

R. LEUNING (*CSIRO Division of Forestry and Forest Products, Canberra, Australia*). Dr Shuttleworth's paper implies that the water storage on forest canopies is approximately the same. Is the total canopy storage dependent on the leaf area index of the canopy? If so, what is the dependence?

W. J. SHUTTLEWORTH. Most experimental studies of forest interception do not have simultaneous measurements of leaf-area index and this is, in part, the reason I have chosen to express the interception store on a per forest stand basis rather than a per leaf-area index basis.

However, Dr Leuning's question gives me the opportunity to comment on the leaf-area dependence of the interception store. Although some relation with leaf-area index is to be expected, many authors assume a proportional relation between these two. I have reservations about doing this. Perhaps the values of interception store for temperate deciduous forest illustrate my point best (see §6*a* and table 1). In this extreme case, changing the leaf-area index from zero in winter to (say) four in summer changes the interception store from about 0.3 mm to 0.8 mm. Clearly water capture by twigs and branches in part compensates for that on the missing foliage. I am fairly sure this level of twig and branch storage does not occur to the same extent when the foliage is present, and it is partly a matter of substituting one water store by another, rather than adding one store to another. To some extent this is likely to be a general feature. I am also uncomfortable with the concept of an interception store which is a measure of the total water a canopy can hold when every surface has been wetted and allowed to drain. Artificial wetting experiments attempt to measure such a conceptual entity, but the value is always larger, sometimes several times larger, than the interception store required to explain measured interception loss with real rainstorms. It is likely that there is some statistical aspect to the effective value of the interception store: that mutual shading will mean not all the leaf and twig area is normally wetted even by heavy and protracted storms. This is likely to moderate the relation between interception storage and leaf area, and generate a relation which is less than proportional.

T. A. BLACK (*Department of Soil Sciences, University of British Columbia, Canada*). Would Dr Shuttleworth please comment further on the possibility of using remote sensing techniques to estimate the course of canopy conductance during the year?

W. J. SHUTTLEWORTH. Before answering this question I must first emphasize the speculative nature of my comments and that any data I present are still very preliminary.

In this paper the canopy conductance for forest stands is expressed as a product of a constant, which is characteristic of the forest, several environmental stress factors, which seem to have reasonably similar form from one stand to the next, and a 'canopy factor' (see equation (7)). This canopy factor describes the joint effect of seasonal variations in leaf-area index, green-leaf fraction and changes in stomatal response associated with foliage age. During the optimization of equation (7) for the four 'calibration' forests (described in §7*a*), the canopy factor, g_C, is set to unity. It is, of course, subsequently possible to use this fitted form of g_s to calculate transpiration. The ratio between this (say) monthly average calculation of transpiration and the measured transpiration for equivalent hours is then a measure of seasonal changes in g_C. Figure d1 (*a*) shows an example of the results of applying this procedure to data from the Amazonian rain forest (Shuttleworth 1988). The remnant seasonal behaviour is not large, being typically 5–10%, but is statistically significant.

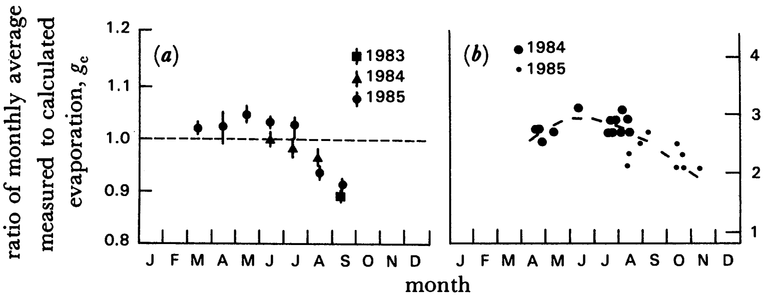

FIGURE d1. (*a*) Seasonal variation in the derived value for the canopy factor, g_C (see equation 7), in the surface conductance of Amazonian rain forest near Manaus, Brazil. (*b*) Seasonal variation in the peak frequency of the probability distribution for the simple ratio derived from NOAA-7 AVHRR data for a region around this Amazonian site.

Certain remote sensing parameters are believed to be a function of the same seasonal controls which determine the factor g_C. In particular, the so-called NDVI, or closely allied 'simple ratio', are a joint measure of leaf-area index and the fraction of green, photosynthetically active leaves (Sellers 1986). They are derived from the difference in whole-canopy reflectance in the visible and near infrared portions of the spectrum. Figure d1 (*b*) shows the seasonal change in the simple ratio derived from NOAA-7 AVHRR satellite data for an area around the experimental site used for collection of the Amazon field data. It is extremely interesting and significant that there is a seasonal change somewhat similar to that in g_C, and this tempts the suggestion that it may be possible to use remote sensing to map out the forest's canopy factor in time and space over the whole biome.

In fact, the two seasonal trends in figure d1 differ in their detailed timing, with the response in simple ratio a few weeks later than that in g_C. My interpretation is that the physiology of forest leaves begins to alter before this becomes apparent optically: that foliage begins to lose its stomatal efficiency before it turns brown and falls from the tree. With this in mind, it is interesting to speculate that other remote sensing parameters in the microwave region may ultimately prove more useful in this context. The so-called microwave polarization difference index (MPDI) (Choudhury 1988) is often considered a measure of foliage water content. It is at least possible that net canopy water content is a better measure of the combined effect of leaf-area index, live–dead leaf fraction and leaf age on surface conductance, and MPDI is therefore a better remote sensing surrogate of the g_C factor in equation (7).

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J. Grace (*Department of Forestry and Natural Resources, University of Edinburgh, U.K.*). Quite a lot of work suggests that tropical forests display much greater variation in water-vapour saturation deficits than temperate forests. This is supposed to result from their greater height and more pronounced in-canopy stratification. Would Dr Shuttleworth give values for such changes?

P. G. Jarvis (*Department of Forestry and Natural Resources, University of Edinburgh, U.K.*). I am also interested in more information on this point. The diagram presented in Dr Shuttleworth's talk gave profiles of temperatures and specific humidity; would Dr Shuttleworth expand on these and say something about the profile of saturation deficit? From the evidence of personal comfort at the ground compared with that on his Amazonian tower, I suspect the specific humidity deficit near the ground is close to zero. This is very different from that in the trunk space of temperate forest with a single overstorey where down draughts through the vegetation from above give rise to significant coupling between the air near the ground and that in the atmosphere.

W. J. Shuttleworth. In fact, this information is already published (Shuttleworth *et al.* 1985) and see figure 7. However, because of the considerable interest expressed in this topic, I also include an additional figure illustrating the daily variation in through-canopy saturation deficit.

It is indeed true that there is a significant decoupling between the saturation deficit at the base of the canopy in a tropical forest during the day. Data taken at five levels during our Amazonian study (Shuttleworth *et al.* 1985) show the deficit at about 1.5 m is not zero, but is typically only about 20–30 % of the value in the canopy and atmosphere above (see figure d2). Mixing seems to occur reasonably effectively down to about two thirds canopy height during the day, but only the upper levels of the canopy show any significant coupling to the

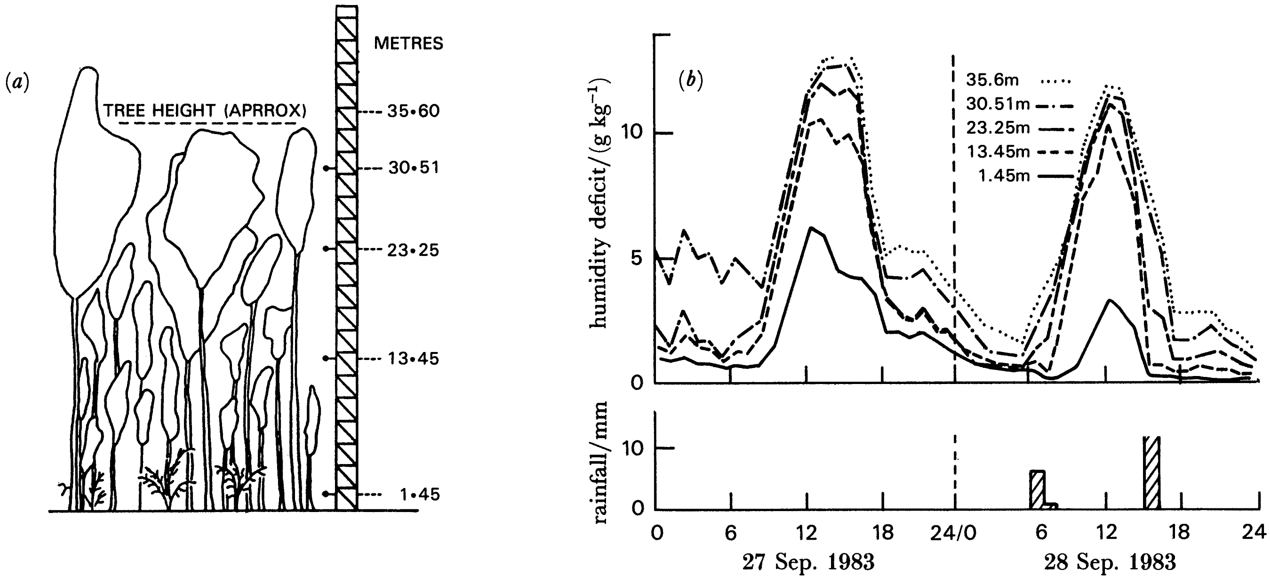

Figure d2. (*a*) Schematic diagram illustrating the five measurement heights through the tropical forest canopy. (*b*) The variation in measured specific humidity saturation deficit at these levels for two successive days with and without rainstorms.

atmosphere at night. During and immediately after rain, the saturation deficit deep in the canopy falls towards zero, but canopy drying is rapid and saturation deficit profiles re-establish their dry canopy behaviour within a few hours.

J. Roberts (*NERC Institute of Hydrology*, *Wallingford*, *U.K.*). Professor Jarvis asked Dr Shuttleworth what would be typical saturation deficit differences throughout the forest at Manaus, Brazil. Our measurements showed that specific humidity deficits as large as 15.9 g kg^{-1} could occur in the upper canopy whereas at the same time on the forest floor the values could be as small as 2.9 g kg^{-1}.

H. G. Jones (*AFRC Institute of Horticultural Research*, *Wellesbourne*, *U.K.*). The equation Dr Shuttleworth presented for prediction of surface conductance contains several independent stress terms. Is there any evidence for interaction terms?

W. J. Shuttleworth. There is sometimes evidence of interaction between stress terms in the stomatal conductance of individual leaves, and it is to be expected that this will be reflected in surface conductance to some extent. It is always possible to provide an 'improved' description of a particular set of experimental data by including additional free parameters. In the case of the work reviewed in this presentation, expressing the surface conductance as a series of independent stress terms was found to provide a description adequate within likely experimental error, and my emphasis here has been to seek simple, common features.