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Discerning the forest from the trees: an essay on scaling canopy stomatal conductance

Dennis D. Baldocchi[a], Robert J. Luxmoore[b] and Jerry L. Hatfield[c]

[a]*Atmospheric Turbulence and Diffusion Division, ARL/NOAA, P.O. Box 2456, Oak Ridge, TN 37831, USA*

[b]*Environmental Science Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, TN 37831, USA*

[c]*USDA/ARS, National Soil Tilth Laboratory, 2150 Pammel Drive, Ames, IA 50011, USA*

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ABSTRACT

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Stomata are major conduits for the diffusion of many trace gases between leaves and the atmosphere. The role of the stomata in controlling gas exchange between the terrestrial biosphere and the atmosphere at the landscape, meso- and global scales has only recently been appreciated. Further advances in modeling trace gas exchange will depend on our ability to provide realistic information on stomatal mechanics at the sub-grid scale of landscape and meso scale models; in other words, information is needed at the canopy scale.

This paper describes two approaches for estimating canopy stomatal conductance. These are the 'bottom-up' and 'top-down' scaling methods. The bottom-up method entails computing canopy stomatal conductance by integrating the response of individual leaves to controling biotic and abiotic factors, which are determined by the micrometeorology of the canopy. The top-down approach entails inverting a descriptive stand-level, trace gas exchange model to estimate canopy stomatal conductance. The model is driven with abiotic variables measured at a reference point above the canopy. The strengths and weaknesses of these two approaches are discussed, and recommendations for future research are presented.

INTRODUCTION

Stomata are openings through which gases diffuse into and out of leaves. They are a major conduit for the transfer of many trace gases between the terrestrial biosphere and atmosphere. Consequently, stomata are a major factor in the biological control of our climate system and the chemistry of our atmosphere.

Stomata affect trace gas exchange between vegetation and the atmosphere across a spectrum of spatial scales. These scales range from the size of a stomate (microns) to those of leaves (centimeters), plants (meters), canopies (tens to hundreds of meters) and landscapes (kilometers). The canopy is the scale that will be discussed in this essay on stomatal conductance. Canopy stomatal conductance is defined as the mean value of the stomatal conductance of individual leaves added in series and weighted by leaf area. Canopy stomatal conductance can be measured directly by porometers, as long as they are implemented correctly in an intensive, stratified, sampling program (Jarvis et al., 1981; Leverenz et al., 1982). It has also been demonstrated that canopy stomatal conductance can be measured by whole-plant chambers (Wong and Dunin, 1987).

Canopy stomatal conductance is an interesting and complex variable. It is determined by leaf-level physiological processes and yet it regulates landscape- and mesoscale trace gas exchange processes relating to atmospheric chemistry, hydrology and climate (Deardorff, 1978a; Dickinson, 1983; McNaughton and Spriggs, 1986; Sellers et al., 1986; Hicks et al., 1987). Some landscape-scale evaporation models (e.g. De Bruin, 1983; McNaughton and Spriggs, 1986) use a canopy stomatal conductance that is computed from the stand-level equation for canopy latent heat exchange (Monteith, 1973), where latent heat exchange is either measured directly or inferred from the surface energy balance. This technique, however, determines the canopy surface conductance, not the canopy stomatal conductance (Stewart and Thom, 1973; Shuttleworth, 1976; Baldocchi et al., 1987; Finnigan and Raupach, 1987). Care should be taken when applying the canopy surface conductance for water vapor exchange as the canopy stomatal conductance for the exchange of another trace gas.

The goal of this paper is to describe canopy stomatal conductance and discuss techniques that can be used to estimate it. Since information on stomata exists across many scales, we will use a hierarchical approach to describe it. The 'bottom-up' and 'top-down' hierarchical approaches are the two methods chosen to attain this goal. The bottom up approach uses mechanistic information to derive canopy stomatal conductance; it is computed by integrating the response of individual leaves to controlling biotic and abiotic factors, which are determined by the micrometeorology of the canopy. The top down approach entails inverting a descriptive stand-level trace gas exchange model to estimate the canopy stomatal conductance.

Several scaling rules must be defined and observed before we can proceed. First, only information from adjacent time and space scales should be used. The number of scales needed to describe a system is, therefore, limited to three: the sub-, operational- and macroscale regimes. The mechanistics and the dynamics of an operational-scale system are described by subscale processes. The state variables that drive the operational- and subscale processes are determined by the macroscale processes. Pertinent information from nonadjacent scales is not desirable because such information is often impractical to obtain, unreliable, noisy and/or insignificant. Case in point: as we move upward and across scales, stomatal conductance needs to be described by an increasing number of subscale variables, which increase simultaneously in spatial and temporal variability. If we want to model the stomatal conductance of a plant canopy, it would obviously be impractical to concern ourselves with the processes on the scale of individual pairs of guard cells, whose aperture varies markedly across a leaf. Fine-scale information will only be important at the macroscale if the system is highly non-linear and is sensitive to small-scale perturbations. On scaling downward, we do not need to model macro-scale processes because their temporal and spatial variability is too small to be of concern at the smaller scales being studied. Macroscale variables are considered to be external to the system and are typically defined as the variables that drive the system; solar radiation, humidity and air temperature measured above a plant canopy are examples of macroscale variables often used to model and interpret canopy stomatal conductance.

Another scaling rule to recognize is that biophysical information does not always transfer linearly between small and large time and space scales. Processes that may be important at some scales may not be important at other scales; e.g. the energy balance of a canopy is directly affected by soil and vegetation heat storage, while the energy balance of a leaf is not. Consequently, we must identify the key processes that are controlling the system at the scale being studied and use only those variables to model the system.

BOTTOM-UP: SCALING FROM A LEAF TO A CANOPY

Stomatal conductance of a leaf

The steady-state, stomatal conductance of a leaf (g_s) responds to photosynthetic photon flux density (Q_p), leaf temperature (T_l), the vapor pressure difference between the leaf surface and the stomatal cavity (Δe), internal CO_2 concentration (C_i) and soil water potential (ψ_s) (Jarvis, 1976; Schulze and Hall, 1982; Mansfield, 1985; Gollan et al., 1986; Schulze, 1986). The stomatal conductance of a leaf is also a function of its age, adaptation to its microenvironment and the diffusivity of the molecule that is transferred through the stomata (Chazdon and Pearcy, 1986; Taylor et al., 1988). Some physiological studies link stomatal control to leaf photosynthesis, internal CO_2 concentration and relative humidity at the leaf surface (Wong et al., 1979; Ball et al., 1987) and to an optimization between changes in assimilation and transpiration (Cowan, 1982). Other researchers conclude that stomatal conductance is independent of the rate of leaf photosynthesis, whereas it is indisputable that leaf photosynthesis depends on stomatal conductance (Jarvis and Morison, 1981).

In this essay, we will use the empirical multiplicative model proposed by

Jarvis (1976) for linking the stomatal conductance of a leaf under natural conditions to that of a canopy (similar models have been presented by Takakura et al. (1975) and Avissar et al. (1985), among others)

$$g_s = g(Q_p) f(T_l) f(\Delta e) f(C_i) f(\psi_s) \tag{1}$$

where $g(Q_p)$ defines the response of stomatal conductance to photosynthetic photon flux density. The other functions incorporate limiting influences attributed to leaf temperature (T_l), vapor pressure differences between the leaf surface and stomatal cavity (Δe), internal CO_2 concentration (C_i) and soil water potential (ψ_s). These functions range in value between zero and one.

The Jarvis model is limited by a lack of considering any interaction or feedback responses. Any of the three following methods can remedy this limitation: (1) use eqn. (1) in an iterative feedback loop with the leaf energy balance; (2) incorporate different functions that include interaction terms (Losch and Tenhunen, 1981); or (3) use an alternative method that includes feedbacks, such as the model attributed to Ball et al. (1987).

Light

It is well established that stomatal conductance responds to light (Jarvis, 1976; Mansfield, 1985; Schulze, 1986). The proposed mechanism involves the direct and indirect use of light energy to drive the proton–potassium ion pump. Opening and closing of the stomata, consequently, occur in response to alteration in the turgor of the guard cells (Jarvis and Morison, 1981). Laboratory studies show that the stomatal conductance of a leaf responds preferentially to blue light (Jarvis and Morison, 1981; Mansfield, 1985). This result suggests that stomata act independently of mesophyll photosynthesis (Jarvis and Morison, 1981). Yet, in spite of these far-reaching results, some workers continue to link stomatal action to leaf photosynthesis (Cowan, 1982; Ball et al., 1987).

For the purpose of modeling, stomatal conductance is commonly expressed as a non-linear function of Q_p

$$g(Q_p) = \frac{g_x Q_p}{Q_p + \beta} \tag{2}$$

where g_x is the maximum stomatal conductance and β is an empirical curvature coefficient.

Dynamic responses of stomatal conductance to light flecks and adaptation effects to sunlight and shade regimes are an important component of stomatal mechanics. For example, it can take in excess of 20 min for maximal stomatal opening to occur in response to a light fleck (Chazdon and Pearcy, 1986; Kirschbaum et al., 1988). Dynamic leaf conductance models are not readily available, fully developed or amenable to scaling. At present, it is unknown what amount of error is introduced by using a steady-state scaling approach and ignoring dynamic effects.

Temperature and humidity

Stomatal conductance responds to temperature in a curvilinear manner. Stomatal action depends on temperature due to the temperature dependency of enzyme activity and the saturation vapor density. Conductances are greatest at an optimum temperature (T_o), which is typically between 20 and 30 °C. Conductances are restricted by either extremely low (T_n) or high (T_x) leaf temperatures, which are approximately 5 and 45 °C, respectively (Jarvis, 1976). A common function for describing the temperature relationship is:

$$f(T_l)=\frac{(T_l-T_x)}{(T_o-T_n)}\Bigg/\frac{(T_x-T_l)^{(T_x-T_o)/(T_o-T_n)}}{(T_x-T_o)} \qquad (3)$$

The stomatal conductance of many plant species decreases as the vapor pressure difference between the leaf surface and its interior increases (Schulze and Hall, 1982; Bunce, 1985; Sanford and Jarvis, 1986; Schulze, 1986; Ball et al., 1987). Simple linear models are often used to describe the effect of humidity differences on stomatal conductance

$$f(\Delta e)=1-k_e\Delta e \qquad (4)$$

where k_e is a constant.

The role of humidity on stomatal conductance is more complicated than is suggested above, owing to feedback and feedforward control loops between transpiration, leaf temperature and vapor pressure gradients (Farquhar, 1978; Jones, 1983; Mansfield, 1985; Schulze, 1986). The following text describes current theory on the interactions between humidity and stomatal conductance. An increasing vapor pressure gradient between the stomatal cavity and leaf surface increases peristomatal transpiration. Thereby, the water status of the guard cells and the stomatal apparatus is affected, causing partial closure of the stomata. Feedback control is evident when this response is followed by a reduction in transpiration and a correction of the water deficit in the guard cells. The role of a feedforward mechanism, according to Jones (1983), is less certain, yet Lösch and Tenhunen (1981) reported that 70 species exhibit feedforward properties. Feedforward control occurs when transpiration remains limited in spite of any correction of the water deficit that may have occurred via feedback effects (Farquhar, 1978). Humidity control on stomatal action is simultaneously modified by a temperature feedback. A reduction in transpiration, associated with partial stomatal closure, can increase the leaf temperature, affecting the temperature control loop and the saturation vapor pressure at the leaf surface.

Soil water deficits

Roots and soil form an integral part of the soil–plant–atmosphere continuum and they can significantly influence stomatal control of transpiration, particularly as the period of wetting and drying cycles lengthens. Longer drying periods cause transpired water to be supplied increasingly from storage within the vegetation (Whitehead and Jarvis, 1981), from soil in the root zone, and from recharge by upward flux from deep soil layers (Luxmoore, 1983) or by lateral flow from adjacent moist zones.

The concept of the soil–plant–atmosphere continuum is well established (Van den Honert, 1948) and whole plant models linking liquid and vapor transport have been developed for a range of soil–plant combinations (Federer, 1979; Feddes, 1981). The hydraulic linkage between the stomata and the soil is described in the following: stomata are embedded in the leaf epidermis which is hydraulically linked to the pathway between leaf and stem xylem elements, between roots and the water films, and between saturated pores of the soil. Leaf water potential is determined by relationships for the liquid pathway that include plant resistances and capacitances, and soil hydraulic properties.

Many models employ a relationship between leaf water potential and stomatal conductance that is based on the empirical observation of an on/off relationship between stomatal conductance and leaf water potential; stomata are apparently independent of water potential above some threshold value (e.g. Boyer, 1970; Schulze and Hall, 1982; Baldocchi et al., 1985).

Some models use a simplified conductance formulation that does not include consideration of plant water status, as in the study by Wetzel and Chang (1988) on soil variability effects on areal evapotranspiration. This approach is based on the rationalization that plant water status is not a controlling variable under non-stress conditions and that soil water status can be used as a driving variable for stress conditions. Van Bavel (1967), Szeicz and Long (1969) and Hatfield (1985), among others, have shown that the canopy stomatal resistance is empirically related to soil water content.

There is growing evidence supporting the idea of a direct effect of soil water status on stomatal activity. Experiments reported by Gollan et al. (1986) showed direct stomatal responses in wheat and sunflower to drying soil. Stomatal closure was not mediated through leaf water status in their experiments and a chemical signal was suspected. Recently, Gollan (1988) reported that stomatal closure in leaves at full turgor was related to abscisic acid (ABA) concentration in the leaf and to ion concentration, pH and ABA levels in xylem sap. Research is actively continuing in this area and may lead to new or modified stomatal response functions. Nevertheless, empirical stomatal conductance–leaf water potential relationships probably already include hormonal signals induced by soil water content, and hormonal controls may turn out to explain the on/off behavior mentioned earlier.

Internal CO_2 concentration

Stomatal conductance decreases with increasing internal CO_2 concentration. The mechanism by which CO_2 controls stomatal opening is still unknown (Pearcy and Bjorkman, 1983). However, Jarvis and Morison (1981) speculate that CO_2 may affect the ion pump that regulates guard cell turgor. Empirical evidence suggests that a control loop exists between stomatal conductance, internal carbon dioxide concentration (C_i) and leaf photosynthesis (A) (Wong et al., 1979; Ball et al., 1987). Yet, one must be careful when interpreting these results. Autocorrelative effects may occur due to the origins of these variables; C_i is often derived from measurements of g_s and A. Jarvis and Morison (1981) showed that the dependency of g_s on internal CO_2 concentration can readily be broken by exposure to blue light. Consequently, they are skeptical of reported dependencies of g_s on C_i.

Canopy stomatal conductance

Canopy micrometeorology: defining the canopy microenvironment

The states of many abiotic variables that govern stomatal mechanics are determined by the fates of incoming and outgoing radiant energy above and within the plant canopy (see Norman, 1979; Campbell, 1982) and by the level of turbulent mixing. Multiple-layer models, describing the micrometeorology and radiative transfer inside plant canopies, provide the framework for computing the vertical profiles of abiotic variables that are used to scale stomatal conductance from a leaf to a canopy (see Waggoner, 1975; Goudriaan, 1977; Norman, 1979; Jarvis et al., 1985; Meyers and Paw U, 1987). Canopy micrometeorology models are derived from the equations that describe the conservation of mass, momentum and turbulent kinetic energy (see Finnigan and Raupach, 1987; Meyers and Paw U, 1987; Wilson, 1989) and the equations that describe the short- and long-wave radiation balance (Norman, 1979; Ross, 1981; Myneni et al., 1989).

Theories are best developed for the case of horizontally homogeneous canopies, exposed to steady-state conditions. Under these conditions, the vertical divergence of the turbulent flux of a scalar ($\partial F/\partial z$), in a controlled volume at any level in the canopy, must equal the diffusive source–sink strength of the foliage and soil. The flux divergence of the turbulent flux is generally parameterized with a resistance–analog relationship. The expressions for the flux divergence of any trace gas, x, in conductance and resistance forms are

$$\frac{\partial F(z)}{\partial z} = -a(z)\,\frac{g_{bx}(z)g_s(z)}{g_{bx}(z)+g_s(z)}\,[\rho_{ax}(z)-\rho_{sx}(z)] \tag{5}$$

$$\frac{\partial F(z)}{\partial z} = -a(z)\,\frac{[\rho_{ax}(z)-\rho_{sx}(z)]}{r_{bx}(z)+r_s(z)} \tag{6}$$

where $a(z)$ is leaf area density, g_{bx} and r_{bx} are the leaf boundary-layer conductance and resistance, respectively, and g_s and r_s are the respective leaf stomatal conductance and resistance. ρ_{sx} and ρ_{ax} are the densities of the scalar inside the stomatal cavity and in the air outside the leaf boundary layer, respectively.

Unfortunately, the flux divergence relationship cannot be integrated, with respect to height, to estimate the local turbulent flux (F) because it represents a system with one equation and two unknowns; i.e. F and the scalar density (ρ_{ax}). Closure schemes must be introduced to obtain an equal number of equations and unknowns to compute F and ρ_{ax}. First- and higher-order closure schemes are generally applied to compute the canopy microclimate.

First-order ('K-theory') models assume that turbulent transfer inside a plant canopy is analogous to molecular diffusion. The turbulent flux is proportional to the product of the vertical gradient of the scalar mixing ratio and a 'turbulent' diffusivity (Waggoner, 1975; Goudriaan, 1977; Norman, 1979). 'K-theory' is valid if the length scales of the turbulence are less than those associated with the curvature of the mean mixing ratio profile (Corrsin, 1974). Gradient-transfer theories often misrepresent turbulent exchange processes inside plant canopies because turbulent exchange is dominated by intermittent, large-scale events (Finnigan and Raupach, 1987) which give rise to countergradient transfer (Denmead and Bradley, 1985; Baldocchi and Meyers, 1988).

Higher-order closure models introduce budget equations for the second-order moments; second-order moments include the turbulent covariances for mass and momentum transfer and velocity variance terms, and the variance terms represent components of turbulent kinetic energy (Wilson and Shaw, 1977; Finnigan and Raupach, 1987; Meyers and Paw U, 1987; Wilson, 1989). Modeling tests show that higher-order closure models can successfully simulate the microclimate of a soybean canopy (Meyers and Paw U, 1987). The strength of higher-order closure models is their ability to simulate countergradient transport inside plant canopies (Wilson and Shaw, 1977). On the other hand, the higher-order closure models are limited by the validity of certain assumptions used to close the system of equations and to quantify terms relating to pressure–velocity interactions, the dissipation of turbulent kinetic energy, wake production and the canopy drag force (see Deardorff, 1978b; Shaw and Seginer, 1987).

The canopy microclimate can also be computed with Lagrangian frame models (Raupach, 1987, 1989); Lagrangian models follow the trajectories of an ensemble of marked fluid parcels as they are advected and diffused by the mean wind and turbulence. The advantage of Lagrangian models over the Eulerian closure models is a more realistic treatment of near- and far-field turbulent diffusion. Disadvantages of Lagrangian models include requirements to have a priori information on the turbulence regime and the vertical distribution of sources and sinks, and the dependency of the source–sink distribution on the local concentration field. Only recently have Lagrangian models been proposed for the exchange of sensible and latent heat in crop canopies (Raupach, 1989; Van den Hurk and Baldocchi, 1990). Lagrangian models are rapidly becoming available for use as a tool to scale stomatal conductance.

Several terms in the budget equations depend on the radiation balance on leaves, so it is necessary to model the flux density of radiant energy inside a plant canopy in time and space. Temporal variability arises from the diurnal march of the sun across the sky and from clouds. Spatial variability of radiant energy streams is greatest in the vertical dimension. This variability stems from the vertical distribution of leaves and their ability to intercept and absorb radiation.

Statistical models are classically used to estimate the radiative transfer regime in closed canopies. These models assume that a plant canopy is a plane-parallel and turbid medium (see Ross, 1981; Myneni et al., 1989). Other common modeling assumptions are: the sun is a point source; the foliage is randomly distributed in space; the azimuthal distribution of leaves is symmetrical; the leaf inclination angle distribution and leaf optical properties are invariant with height, and light is scattered isotropically.

The probability of a ray of light passing through a layer of foliage is a function of the angle between the incoming light ray and the mean leaf normal. This probability also depends on the amount of foliage through which the ray must pass. The probability of light penetration is described with a Poisson distribution under ideal conditions (Ross, 1981). The modeling assumptions, described above, are often valid for continuous agricultural crops. The structure of many closed natural stands, on the other hand, is often non-ideal. Leaves are not always distributed randomly in space, but are clumped. Their inclination angles and optical properties can also vary with depth into the canopy (Norman and Jarvis, 1975; Hutchison and Baldocchi, 1989). The scattering of light in plant stands is often anisotropic, due to the bidirectional scattering properties of leaves (Norman et al., 1985; Myneni et al., 1989). In taller vegetation, such as forests and orchards, penumbral effects are consequential because the sun is not a point source; penumbral shade occurs when a foliage element partially obscures the solar disk as seen from a given point below (see Denholm, 1981; Myneni et al., 1989). If the plant stand does not form a closed canopy, the geometric dimensions of the crown and the spatial pattern of the array of plants must be considered (see Jackson, 1980; Norman and Welles, 1983).

Linking the leaf to the canopy

Leaves are exposed to a spectrum of radiation flux densities because of their vertical and angular position in a canopy, and their exposure to sunlit, shaded and partial-shaded regimes. This makes scaling the non-linear stomatal response to photosynthetically active radiation (PAR), leaf temperature and humidity differences very complex in a plant canopy. Equation (1) is scaled from a leaf to a canopy ($\boldsymbol{g}_s$) by serially integrating the response of leaves according to the proportion that are exposed to full sun, full shade and penumbral shade classes, and the radiation load on leaves in those classes

$$\begin{aligned}\boldsymbol{g}_s = \int_0^L & g_s(Q_{ps} T_{ls} \Delta e_s) P_s(L') + g_s(Q_{pu} T_{lu} \Delta e_u) P_u(L') \\ & + g_s(Q_{pp} T_{lp} \Delta e_u) P_u(L') \mathrm{d}L' \end{aligned} \tag{7}$$

The subscripts s, u and p identify the photosynthetic photon flux density (Q_p), leaf temperatures (T_l) and vapor pressure differences (Δe) that are associated with the sunlit (P_s), umbral (P_u) and penumbral (P_p) fractions of leaf area (L). To account for shade and age adaptation features, the model coefficient used to compute stomatal conductance in eqn. (1) can be altered accordingly.

A canopy radiative transfer model must be used to compute Q_p and sunlit, shaded and penumbral leaf area fractions in a canopy (see Norman, 1979; Ross, 1981; Myneni et al., 1989). The effects of internal CO_2 concentration and soil water potential are omitted from eqn. (7), but they can be easily included, as is shown in eqn. (1).

The statistical, parallel-plane, canopy radiative transfer theory, discussed above, cannot be used to scale the dynamic response of leaves to sunflecks. If we are to include light dynamics, we must use a different approach. We must simulate, in time and space, the light environment on individual leaves and couple these computations to a dynamic stomatal conductance model, such as the one proposed by Kirschbaum et al. (1988). The procedural model of Myneni and Impens (1985) is capable of simulating the radiation environment on individual leaves. Unfortunately, the data requirements for operating such a model are tremendous; for example, one must know the three-dimensional spatial distribution and orientation of leaves in a plant canopy. One can circumvent this tremendous data requirement by assuming a probability distribution for the leaves' position (see Ross, 1981) and then randomly assigning them a spatial position and orientation with a Monte-Carlo scheme.

Leaf temperature and humidity are determined from the balance between net incoming short- and long-wave radiation, and its partitioning into sensible and latent heat exchange

$$\boldsymbol{R}_t - \epsilon\sigma T_l^4 = \rho_a c_p \frac{(T_l - T_a)}{r_{bh}} + \lambda\rho_a \frac{[w^*(T_l) - w]}{r_{bv} + r_s} \tag{8}$$

where $\boldsymbol{R}_t$ is absorbed incoming long- and short-wave energy, ϵ is emissivity and σ is the Stefan–Boltzmann constant. ρ_a is air density, c_p is the specific heat of air, $w^*(T_l)$ is the saturation mixing ratio at the leaf temperature (T_l), w is the vapor mixing ratio of the air, T_a is air temperature and λ is the latent heat of vaporization. r_{bh} and r_{bv} are the leaf boundary-layer resistances to heat and vapor transfer, respectively, and r_s is the stomatal resistance for water vapor transfer. Equation (8) is derived on the assumption that energy consumed by leaf photosynthesis and heat storage is negligible. Leaf temperature can be estimated using any of the following methods: (1) an iterative scheme based on Newton's method (Bristow, 1987); (2) an analytical method (Paw U and Gao, 1988), or (3) by linearizing eqn. (8) (Campbell, 1977).

TOP-DOWN DETERMINATIONS OF CANOPY STOMATAL CONDUCTANCE

A simple, stand-level or 'big-leaf' model can be inverted to estimate canopy stomatal conductance if certain conditions are met. These conditions include: a steady-state environment; a dry, fully developed, horizontally homogeneous canopy situated on level terrain; identical source–sink levels for water vapor, sensible heat and momentum transfer, and negligible cuticular transpiration and soil evaporation.

The stand-level estimate of canopy latent heat exchange ($\lambda \boldsymbol{E}$) is

$$\begin{aligned}\lambda \boldsymbol{E} &= \rho_a \lambda \frac{\boldsymbol{g}_s \boldsymbol{g}_{bv}}{\boldsymbol{g}_s + \boldsymbol{g}_{bv}} [w^*(T_c) - w] \\ &= \rho_a \lambda \frac{[w^*(T_c) - w]}{r_s + r_{bv}}\end{aligned} \tag{9}$$

where $\boldsymbol{g}_s$ and $\boldsymbol{g}_{bv}$ are the 'big-leaf' stomatal and boundary-layer conductances for water vapor exchange, $w^*(T_c)$ is the saturation vapor mixing ratio evaluated at the mean aerodynamic canopy temperature (T_c) and w is the vapor mixing ratio measured at a reference height above the canopy. Note that the conductances in eqn. (9) are additive in parallel. However, when they are expressed in terms of their respective resistances ($\boldsymbol{r}$, the inverse of conductance) they are additive in series.

The mean aerodynamic surface temperature is a function of sensible heat flux ($\boldsymbol{H}$) and the canopy aerodynamic conductance to heat transfer ($\boldsymbol{g}_{bh}$)

$$\boldsymbol{H} = \rho_a c_p \boldsymbol{g}_{bh} (T_c - T_a) \tag{10}$$

Equations (9) and (10) form a coupled set from which $\boldsymbol{g}_s$ and T_c can be solved as long as independent estimates of $\lambda \boldsymbol{E}$, $\boldsymbol{H}$, $\boldsymbol{g}_{bv}$ and $\boldsymbol{g}_{bh}$ are available. An implied assumption in applying eqns. (9) and (10) to calculate $\boldsymbol{g}_s$ is that the same mean aerodynamic canopy temperature drives sensible heat flux and determines the saturation vapor pressure of the canopy, which drives latent heat exchange; hence energy exchanges at the soil are negligible.

λE can be measured directly with a lysimeter. Lysimeters are accurate if the vegetation, soil texture and soil hydraulic properties on the lysimeter are representative of the surrounding field (see Tanner, 1967). λE and H can also be measured or inferred from micrometeorological flux measurements or from measurements of the surface energy balance. The eddy correlation and flux-gradient micrometeorological techniques are accurate to within 20% as long as the terrain is level, the surface is extended and homogeneous, ambient conditions are non-varying, and instrumentation and sampling specifications are met (see Tanner, 1967; Kanemasu et al., 1979; Baldocchi et al., 1988). Inferential energy balance estimates of latent and sensible heat exchange are derived from remote sensing methods (Verma et al., 1976; Hatfield, 1983, 1985; Hatfield et al., 1984; Jackson, 1985; Choudhury et al., 1986; Huband and Monteith, 1986; O'Toole and Real, 1986; Taconet and Vidal-Madjar, 1988; Dunin et al., 1989). Components of the surface radiative energy balance, including radiative surface temperature and reflected short- and long-wave radiation, are measured with sensors on remote platforms. Air temperature and the canopy aerodynamic conductance are made with ground-based measurements. λE is estimated as the residual of the surface energy balance. The emissivity of the canopy must be known and the mean radiative canopy temperature must equal the canopy aerodynamic temperature to obtain a reliable estimate of λE.

Landscape-scale estimates of λE and H have also been used to estimate g_s. Information on the growth of the planetary boundary layer (PBL), entrainment and advection are needed to evaluate regional surface latent heat flux and surface conductance (see Carlson et al., 1981; De Bruin, 1983; McNaughton and Spriggs, 1986). Landscape measurements of λE and H, and measurements of advection and PBL growth, are best made with profiler systems and airplanes (Matson and Harris, 1988; Desjardins et al., 1989).

The boundary-layer conductance (g_{bx}) represents the ability of heat and mass (as denoted by the subscript x) to pass from the effective surface of the canopy to a reference level above the canopy in the turbulent boundary layer. g_{bx}, for a uniform canopy, is expressed as

$$g_{bx} = \frac{k u_*}{\ln\left(\frac{z-d_x}{z_0}\right) - \psi\left(\frac{z}{L}\right) + \ln\left(\frac{z_0}{z_x}\right)\left(\frac{\mathrm{Sc}}{\mathrm{Pr}}\right)^{0.66}} \qquad (11)$$

where d_x is the zero plane displacement height and represents the mean centroid height of mass or heat transfer. z_0 and z_x are the roughness lengths for momentum and mass or heat transfer, respectively. Sc is the Schmidt number, Pr is the Prandtl number, k is von Karman's constant, u_* is friction velocity, ψ is a diabatic correction function and L is the Monin–Obuhkov scale length. The first term on the right-hand side represents the boundary-layer conductance to momentum transfer. The second term represents the quasi-laminar conductance for the transfer of mass or heat. The second term is introduced because momentum transfer is augmented by pressure forces which have no role in heat and mass transfer (see Thom, 1975; Verma and Barfield, 1979).

Measurements of d_x and z_0 can be obtained from wind speed profiles. In homogeneous vegetation stands, d_x is typically $0.6h$ and z_0 is $0.1h$, where h is canopy height (see Monteith, 1973). Fewer values are available for heat and mass transfer over partial canopies. Hatfield (1989) showed that the roughness length and zero plane displacement height vary non-linearly with the height-to-width ratio of a cotton crop. Defining d_x for heat and mass transfer is problematic because it can vary with atmospheric stability (Raupach, 1979). The value of d_x is also affected by factors such as the mean angle between the sun and leaves. Leaf–sun orientation affects the vertical distribution of solar radiation and the magnitude and vertical distribution of stomatal conductance and, consequently, affects the mean source–sink levels of latent and sensible heat (Paw U and Meyers, 1989). The ratio $\ln(z_0/z_x)$ for an extended closed canopy approximately equals 2 (Garratt and Hicks, 1973). Measurements of u_* are obtained from measurements of the covariance in streamwise and vertical velocity fluctuations or wind speed profiles.

Can we estimate the canopy stomatal conductance with the Penman–Monteith model?

The Penman–Monteith equation for latent heat exchange can be derived by combining resistance–analog equations for sensible and latent heat exchange and the energy balance relationship (Monteith, 1973). Its elegance and usefulness are based on the algebraic elimination of surface temperature

$$\lambda \boldsymbol{E}=\frac{s(\boldsymbol{R}_{\mathrm{n}}-\boldsymbol{G})+\rho_{\mathrm{a}}c_{\mathrm{p}}\boldsymbol{D}\boldsymbol{g}_{\mathrm{bv}}}{s+\gamma\left(1+\dfrac{\boldsymbol{g}_{\mathrm{bv}}}{\boldsymbol{g}'_{\mathrm{s}}}\right)} \tag{12}$$

where s is the slope of the saturation vapor pressure–temperature curve, γ is the psychrometric constant, $\boldsymbol{R}_{\mathrm{n}}$ is net all-wave radiation flux density, $\boldsymbol{G}$ is soil heat flux density, D is the vapor pressure deficit at the reference level above the canopy. $\boldsymbol{g}'_{\mathrm{s}}$ is the canopy surface conductance. We denote $\boldsymbol{g}'_{\mathrm{s}}$ with a prime to distinguish it from the canopy stomatal conductance that is used in eqn. (7).

The canopy surface conductance computed from the Penman–Monteith equation ($\boldsymbol{g}'_{\mathrm{s}}$) and the canopy stomatal conductance that is derived from the product of leaf porometry and leaf area index measurements are often used interchangeably (Jarvis et al., 1981). Computations of $\boldsymbol{g}'_{\mathrm{s}}$ in a deciduous forest from a soil–plant–atmosphere continuum model (Luxmoore, 1978; Fig. 1) and field measurements of energy exchange (e.g. Verma et al., 1986) show that the diurnal course of g_s' mimics the behavior of individual leaves (Hinckley et al., 1981). Yet, it is shown both theoretically (Stewart and Thom, 1973; Shuttleworth, 1976; Finnigan and Raupach, 1987; Paw U and Meyers, 1989) and experimentally (Baldocchi et al., 1987) that these two measures of canopy stomatal conductance may not be equal. g_s' contains additional non-physiological information pertaining to the net radiation balance and the aerodynamic conductances inside the canopy (Stewart and Thom, 1973; Finnigan and Raupach, 1987). Under field conditions, estimates of g_s' are also contaminated by the reality that soil evaporation is generally non-zero.

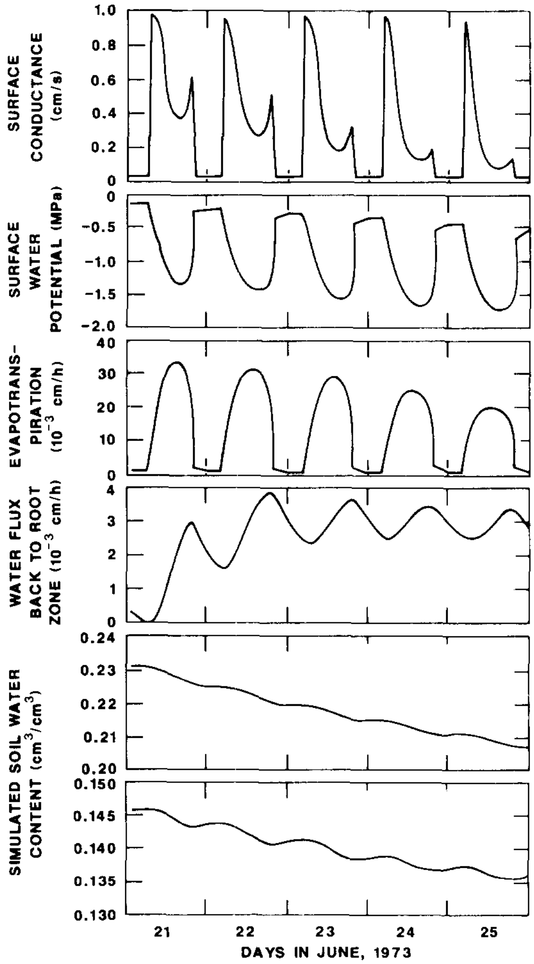

Fig. 1. Simulated plant and soil water dynamics of a yellow poplar stand during a 5-day drying period following rainfall (after Luxmoore et al., 1978).

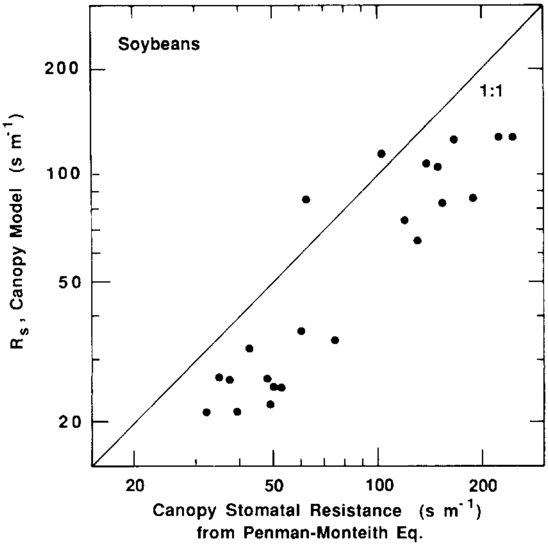

Fig. 2. Comparison of integrated canopy resistance (R_s) and values computed with the Penman–Monteith equation (R'_s). These data are for soybeans (adapted from Baldocchi et al., 1987).

Figure 2 shows a comparison between canopy stomatal resistances (the inverse of the conductances) computed with the 'bottom-up' technique, described above, and the Penman–Monteith equation. Clearly, the two methods differ markedly. Independent tests show that the stomatal conductances computed with the bottom-up technique agree well with porometer measurements of canopy stomatal resistance (Norman, 1982; Baldocchi et al., 1987), thus the bottom-up technique represents a better estimate of the true canopy stomatal resistance. Finnigan and Raupach (1987) reported that the ratio between g_s and g'_s differs significantly from one. The ratio ranges between 0.4 and 1.3, depending on the aerodynamic roughness of the canopy and the degree of stomatal opening. We stress that g'_s in the Penman–Monteith equation represents the canopy surface conductance to water vapor exchange. It generally does not equal the canopy stomatal conductance, but it does contain information relating to the opening of the stomata.

Estimating g_s *under non-ideal conditions*

The validity and accuracy of estimating canopy stomatal conductance from eqns. (9)–(11) are often limited by natural variations in vegetation, topography and the ambient environment. Limitations are caused by incomplete canopy cover, a separate understory canopy, terrain complexities, heterogeneities in the physiological, radiative and aerodynamic characteristic of the upwind vegetation, and temporal trends in ambient conditions. $\lambda \boldsymbol{E}$, $\boldsymbol{H}$, T_c and $\boldsymbol{g}_{bv}$ are not the desired quantities for estimating canopy stomatal conductance under non-ideal conditions. $\lambda \boldsymbol{E}$ and $\boldsymbol{H}$ represent the sum of the latent and sensible heat exchange, respectively, from the foliage and soil. $\boldsymbol{g}_{bv}$ represents the aerodynamic conductance of water vapor from the vegetation and soil. T_c represents the aerodynamic surface temperature due to sensible heat exchange from the foliage and soil. T_c will not represent the aerodynamic foliage temperature (T_f) that is needed to compute $\boldsymbol{g}_s$ if substantial heating at the soil surface is occurring or the source levels of canopy sensible and latent heat exchange are not co-located, a condition commonly observed in partial canopies.

Under non-ideal conditions, $\boldsymbol{g}_s$ should be evaluated in terms of the latent heat exchange ($\lambda \boldsymbol{E}_f$) and the aerodynamic temperature and conductance of the canopy foliage. Below we discuss the processes that affect the estimate of canopy stomatal conductance. We also discuss the factors that confound the relevance of using measurements and estimates of $\lambda \boldsymbol{E}$, T_c and $\boldsymbol{g}_{bv}$ to compute $\boldsymbol{g}_s$, and describe means for dealing with confounding complexities.

The mean aerodynamic foliage temperature can be derived using a two-layer, resistance–analog description of the canopy–soil system (Shuttleworth and Wallace, 1985; Smith et al., 1988)

$$\rho_a c_p (T_f - T_a) = \frac{(\boldsymbol{H}_f - \boldsymbol{H}_s)}{\boldsymbol{g}_{bh}\,(\text{soil})} + \frac{\boldsymbol{H}_f}{\boldsymbol{g}_{bh}\,(\text{foliage})} \tag{13}$$

where the aerodynamic conductances for sensible heat transfer between the soil and the atmosphere, and the aerodynamic conductances for sensible heat transfer between the canopy and the atmosphere, are considered separately. The subscripts f and s denote the foliage and soil components of the energy flux densities. If T_f is known, $\boldsymbol{g}_s$ can then be solved from the expression for $\lambda \boldsymbol{E}_f$

$$\lambda \boldsymbol{E}_f = \rho_a \lambda \frac{\boldsymbol{g}_s \boldsymbol{g}_{bv}\,(\text{foliage})}{\boldsymbol{g}_s + \boldsymbol{g}_{bv}\,(\text{foliage})} [w^*(T_f) - w] \tag{14}$$

where $\boldsymbol{g}_{bv}$(foliage) is the aerodynamic conductance for water vapor transfer between the foliage and the atmosphere. To solve eqns. (13) and (14), we must evaluate the canopy energy balance and its partitioning of available energy into latent and sensible heat exchange of the foliage and soil

$$(1-\alpha)\boldsymbol{R}_s + \boldsymbol{R}_l - \epsilon\sigma T_c^4 - \boldsymbol{M} - \boldsymbol{J} - \boldsymbol{G} - \mu \boldsymbol{A} = \lambda \boldsymbol{E}_f + \lambda \boldsymbol{E}_s + \boldsymbol{H}_f + \boldsymbol{H}_s \tag{15}$$

where $\boldsymbol{R}_s$ and $\boldsymbol{R}_l$ are the incoming short-wave and long-wave radiation flux densities, α is albedo, $\boldsymbol{M}$ represents the advection of sensible and latent heat and can either add or remove energy, and $\boldsymbol{G}$ is the soil heat flux density. $\boldsymbol{M}$ is defined as the integration with respect to height of the divergences of the horizontal fluxes of sensible and latent heat. J is the amount of energy consumed or released by physical heat storage of the canopy biomass and its air space. μA represents the energy that is biochemically stored via photosynthetic fixation.

Below we use eqns. (13)–(15) as a framework for discussing g_s. We also discuss how real-world complexities affect the estimate of the variables in these equations.

Available energy

The latent and sensible heat exchange measured at a point represents an integration of the contribution by vegetative sources at varying distances upwind (Leclerc and Thurtell, 1990; Schuepp et al., 1990). The available energy measured at a tower, where micrometeorological flux measurements are often made, will not reflect the available energy that is controlling latent and sensible heat exchange if the physiological, radiative and aerodynamic properties of the upwind vegetation vary spatially or if the radiation balance of upwind fetch is affected by clouds or terrain (see Nunez, 1980). The available energy used to evaluate λE_f, T_f and g_s must correspond to the upwind area where the latent and sensible heat exchange originates if we are to accurately estimate g_s. Case in point: Verma et al. (1986) showed that the net radiation balance can only be closed to within ±30% over a deciduous forest in sloping terrain when using a single-point measure of net radiation on days with variable clouds. Yet, they are able to close the energy balance to within ±10% over flat terrain subjected to clear skies (Anderson et al., 1984). These results suggest that a spatially averaged measure of net radiation is needed to adequately close the energy balance at a complex site under varying conditions.

Advection is defined as the mean transport of a scalar by the motion of the atmosphere. Evaporation from vegetation will be enhanced or suppressed if drier or moister air is, respectively, advected through the control volume (see McNaughton and Jarvis, 1983; Philip, 1987). Advection on scales of regions, fields and inter-row spacing can influence the latent and sensible heat exchange of a plant canopy. Regional-scale advection is due to regional variations in landscape and meteorology. Irregular terrain, shadows by clouds, wet 'footprints' by scattered thunderstorms, land–sea circulations and horizontal gradients in available soil water all cause regional-scale advection. Local-scale advection is primarily the result of differences in the roughness and evaporation potential of adjacent fields. The advection of hot dry air over an actively transpiring surface considerably increases the latent heat exchange of the downwind surface (Philip, 1987). Inter-row advection is significant when crop canopies have not achieved full cover. Under these conditions, excess sensible heat generated between rows can be advected laterally to enhance the evaporation of the row crop (Hanks et al., 1971; Graser et al., 1987).

Soil heat flux density depends on the amount of energy at the soil surface and the soil thermal conductivity; the latter depends on soil density, mineral composition, organic matter, water content and temperature (Kimball and Jackson, 1979). A survey of studies shows that G decreases exponentially from 50 to 5% of net radiation (R_n) as the surface advances from bare to full vegetation (Choudhury et al., 1987). Although soil heat flux can be measured with soil heat flux plates (Kimball and Jackson, 1979), an adequate number of properly spaced sensors is needed to reduce the sampling error due to variability in soil properties and the variability in available energy under partial canopies.

Canopy heat storage is generally small for short vegetation, but can be of the order of 5–10% of net radiation in forest canopies (McCaughey, 1985; Moore and Fisch, 1986). Photosynthetic storage in crop and forest stands is typically $<5\%$ of incoming solar radiation (Loomis and Williams, 1963; Verma et al., 1986).

Latent heat exchange at the soil surface

Soil latent heat exchange is a function of the amount of soil wetness and the amount of energy that is available below the plant canopy. λE_s under a closed canopy is typically $<5\%$ of R_n when the soil is dry (Shuttleworth and Wallace, 1985; Baldocchi et al., 1986). On the other hand, the soil can account for as much as half of the canopy evaporation when the crop is sparse and the soil is wet (Denmead, 1984; Shuttleworth and Wallace, 1985). The maximum rate of soil evaporation decreases proportionally with the square root of the inverse of time after the last precipitation event. Energy released by the soil or advected between rows can also contribute to soil evaporation. Leaf detritus at the soil surface can limit soil evaporation since it acts as a mulch. Hence, most of the water evaporated at the soil surface is derived from the detritus and the underlying soil stays moist (Denmead, 1984).

Foliage temperature

Many scientists have attempted to estimate the aerodynamic canopy temperature with measurements of the canopy radiative temperature using thermal radiometers on ground-based, aircraft and satellite platforms (Heilman et al., 1976; Hatfield, 1983; Choudhury et al., 1986; Huband and Monteith, 1986; Taconet et al., 1986; Smith et al., 1988; Taconet and Vidal-Madjar, 1988; Stewart et al., 1989). The evolving literature shows that the aerodynamic canopy temperature of agricultural crops and forests, determined with ground-based radiometers (Choudhury et al., 1986; Huband and Monteith, 1986; Dunin et al., 1989; Stewart et al., 1989) and aircraft-mounted thermal scanners (Heilman et al., 1976), does not equal the canopy radiative temperature. Figure 3 emphasizes this point with data measured over a fully leafed deciduous forest. Consequently, the errors in estimating canopy latent and sensible heat exchange from such measurements, as needed to estimate g_s, can be large (Verma et al., 1976; Hatfield, 1983; Choudhury et al., 1986; Huband

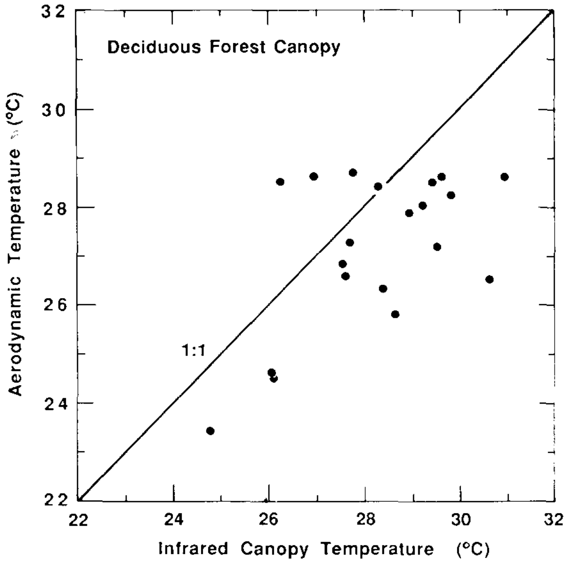

Fig. 3. Comparison between the aerodynamic and radiative temperature of a fully leafed deciduous forest (August 1986). Infrared temperatures were measured with an infrared radiometer positioned above the forest. The radiometer was inclined at 45° and rotated about a 360° axis to obtain a representative integrated canopy temperature. Sensible heat flux was measured with the eddy correlation technique (after D.D. Baldocchi and T.P. Meyers, unpublished results, 1986).

and Monteith, 1985, 1986). The differences between the radiative and aerodynamic temperatures are typically on the order of 2–6°C. Sensitivity tests with the surface energy balance show that a 1°C error in the surface-to-air temperature difference can yield a 40 W m^{-2} error in the estimate of λE. Atmospheric stability determines whether radiative canopy temperature measurements will over- or underestimate aerodynamic canopy temperature (Heilman et al., 1976; Verma et al., 1976; Choudhury et al., 1986).

Representative estimates of the canopy aerodynamic temperature measured with radiometers are difficult to attain because radiative temperature measurements depend on view and sun angles, degree of crop cover, soil–canopy temperature differences and (for airplane- and satellite-mounted sensors) atmospheric attenuation of radiation and the spatial variability in canopy emissivity (Heilman et al., 1976; Kimes et al., 1980; Kimes, 1983; Huband and Monteith, 1986). Nadir-viewed radiometric measurements of canopy temperatures are the least representative of aerodynamic temperatures since radiative measurements are highly biased by the emission of thermal radiation from the soil (Kimes et al., 1980). More representative estimates of the radiative temperature of the foliage are possible by measuring canopy radiative temperature from multiple viewing angles or using the model inversion technique of Kimes (1983).

Nevertheless, several attempts have been made to estimate canopy stomatal conductances from radiometric measurements of canopy temperature. Smith et al. (1988) found that estimates of g_s (determined from surface temperature measurements made with a hand-held radiometer) agree well with estimates of canopy stomatal conductance based on porometer measurements in a dry, high-radiation environment. They used a two-layer model to assess g_s and made an effort to measure the radiative temperature of the foliage by viewing the crop with the radiometer inclined at 45°. On the other hand, Huband and Monteith (1986) and Dunin et al. (1989) found that estimates of latent and sensible heat exchange derived from infrared temperature measurements were unreliable; consequently, derived estimates of g_s are also unreliable.

Surface temperatures measured with the advanced, very high resolution radiometer (AVHRR) satellite and an inverted boundary-layer model have also been used to estimate the foliage resistance to water vapor transfer (Carlson et al., 1981; Price, 1982; Taconet et al., 1986). The ability to measure surface temperature accurately with satellite data is confounded by spatial variability in canopy emissivity, a nadir viewing angle, the inaccuracy of atmospheric corrections and the need for clear skies. For example, Taconet and Vidal-Madjar (1988) note that the on-board calibrator of the AVHRR satellite has

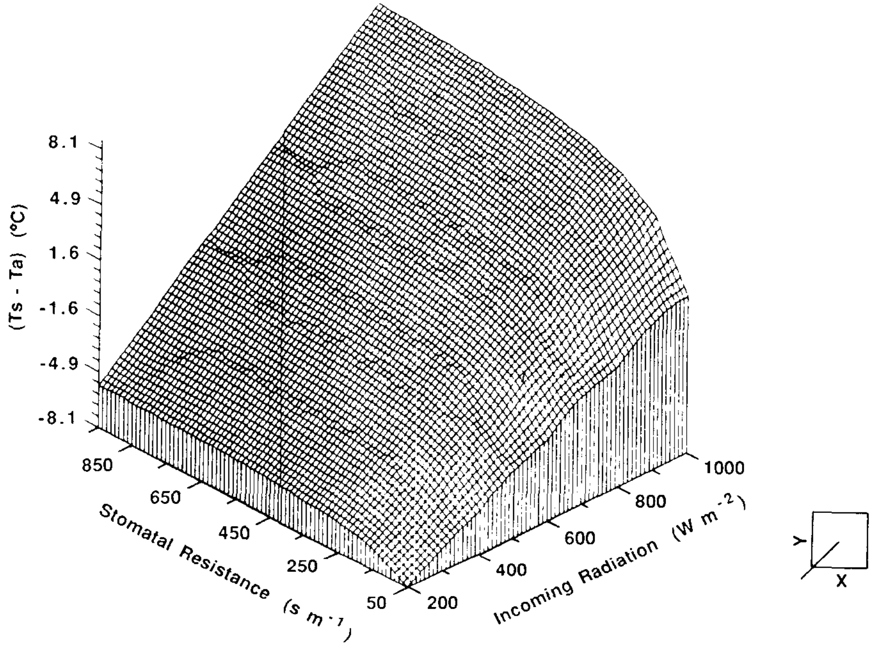

Fig. 4. Stomatal resistance (the inverse of conductance) as a function of surface–air temperature differences and incoming radiation. Humidity was assumed constant at 15 g kg^{-1}.

a 1 °C error and that errors in the surface emissivity can yield a 1–3 °C temperature bias. The inversion schemes must also rely on valid determinations of some surface variables, such as soil heat flux, soil evaporation and surface winds, to provide reliable estimates of λE_f and g_s. 'Reasonable' results have been reported when computations have been compared with surface flux measurements. However, good results have often been fortuitous due to canceling errors. Flux estimates are less sensitive to errors in canopy stomatal conductance than vice versa (Finnigan and Raupach, 1987).

The ability to accurately assess g_s from radiative measurements of surface temperature is limited by the sensitivity of g_s to air–canopy temperature differences. The sensitivity of canopy stomatal resistance $(1/g_s)$ to surface–air temperature differences is demonstrated in Fig. 4 at varying incoming radiation levels and in Fig. 5 at varying humidity levels; these computations are based on the non-linear, surface energy balance relationship (Bristow, 1987). Stomatal resistance is most sensitive to $(T_s - T_a)$ when the flux density of

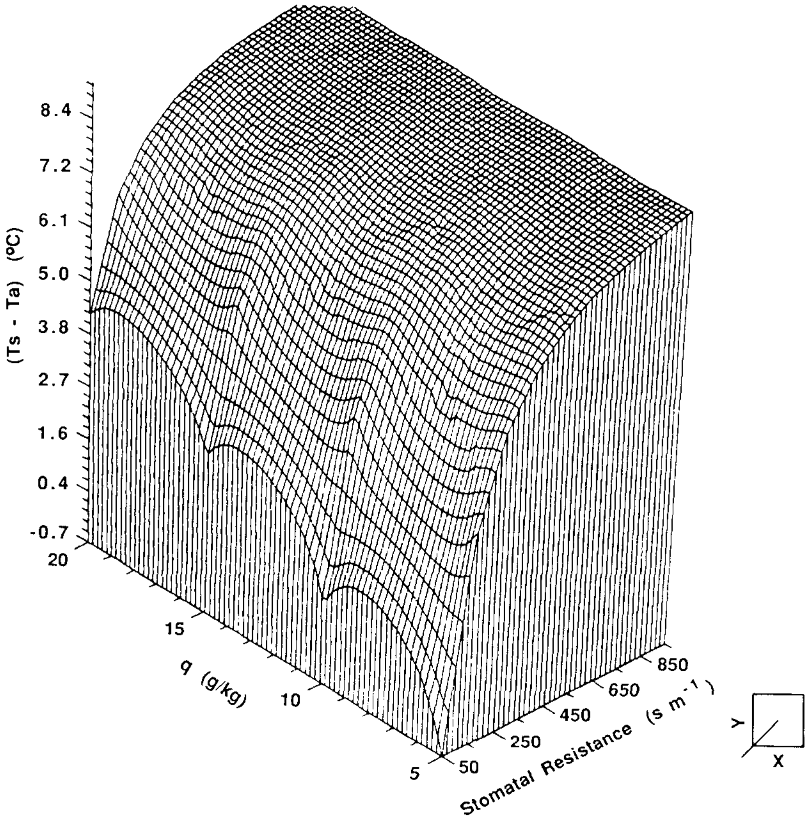

Fig. 5. Stomatal resistance (the inverse of conductance) as a function of surface–air temperature differences and humidity. Incoming radiation was assumed constant at 1000 W m^{-2}.

incoming radiation is high, the air is dry and the canopy is well watered. On the other hand, estimates of $\boldsymbol{r}_s$ derived from remotely sensed data are most susceptible to error under humid cloudy conditions or when the crop stand is water stressed; when $\boldsymbol{R}_s$ exceeds 650 s m^{-1}, a 1 °C change in surface–air temperature differences corresponds to a 200 s m^{-1} change in $\boldsymbol{R}_s$. These modeling results help explain the favorable results reported by Smith et al. (1988) in Australia and the unfavorable results reported by Huband and Monteith (1986) in England. We, thereby, advise caution in using radiative temperatures to estimate $\boldsymbol{g}_s$.

Boundary-layer conductance

For sparse canopies and hedgerows, the ratio $\ln(z_0/z_x)$ is not well behaved (eqn. (11)). Values for sparse canopies and hedgerows range between 2 and 20 (Garratt and Hicks, 1973; Kustas et al., 1989). This theory is not well behaved for incomplete canopies because turbulence structure becomes three-dimensional. Three-dimensional flow and discontinuous source/sink distributions over partial canopies make the applicability of such concepts as roughness length and zero-plane displacement tenuous. Unfortunately, the theory on three-dimensional flow in plant canopies is not well developed to remedy this problem.

DISCUSSION AND CONCLUSIONS

The literature on canopy stomatal conductance contains both complex and simple estimation schemes. Which schemes are best? Which schemes should we use?

The 'top-down' approach is attractive since it is integrative and is based on simple and general laws. Another advantage is its requirement for few, simply measured input variables. Simple integrative approaches, however, are valid only if they are used under the conditions for which they were derived. Adaptations to the 'big-leaf' model must be made if it is used in other circumstances. When studying the biological control of trace gas exchange, it is particularly important to extract the stomatal conductance instead of the surface conductance from a 'big-leaf' water vapor exchange model. This is because the pathways for trace gas exchange will be different from that of water vapor; the latter can have a significant soil component.

Reductionist models are generally used as research tools for describing and understanding a system in as great detail as possible. Bottom-up models can provide valuable detail on the canopy microclimate, which is needed to drive model parameterizations. This information is especially important when a given parameterization depends non-linearly on its independent variable. If reductionist models are used in an applied mode, simplifications will be needed. Simplifications should be based on sound science, derived from detailed reductionist studies and sensitivity tests.

A difficulty in scaling-up is choosing proper mathematical relationships between stomatal action and governing abiotic variables; in biology one can often find an exception where a specific relationship is not applicable. Much confusion in the literature stems from the choice of a reference level at which the governing abiotic variables are measured and by the artificiality of well-stirred cuvette measurements (see Bunce, 1985). Studies exist that have quantified stomatal action according to the environment above the canopy, inside the canopy airspace, and outside and inside the boundary layer adjacent to leaves (Bunce, 1985; Ball et al., 1987; Idso et al., 1988; Monteith, 1990). Stomata respond to the environmental condition at the leaf surface and not at the other mentioned locations. Appreciable error may occur if a leaf is strongly decoupled from the environment above and within the canopy. Much confusion regarding this issue will be reduced by measuring and modeling conditions at the leaf surface.

Recommendations for research

To estimate landscape-scale stomatal conductance, the advection problem needs to be revisited. Information is needed on the role of field size and complexity of the landscape mosaic in estimating the average landscape trace gas exchange rate and stomatal conductance. Studies on this question are needed to improve the parameterization of sub-grid scale processes in global circulation models (GCM) and regional meso-scale models.

Partial plant cover is more the rule than the exception over most of the year. More measurements and models are needed to describe three-dimensional turbulence exchange in plant canopies so we can assess the role of incomplete plant cover on mass and energy exchange. We need to know if and how we can parameterize the stand-level aerodynamic conductance to heat and mass transfer over sparse canopies. If we are to use a two-layer model to estimate g_s, we must also know how to evaluate the separate aerodynamic conductances of the foliage and soil. The role of inter-row advection on canopy evaporation also needs further study. Inter-row temperature gradients in sparse canopies can often exceed 20°C over the distance of 0.5 m, thus supplying a substantial amount of energy to the evaporative process.

Reductionist scaling is a function of our ability to model the canopy microclimate. Further development of analytical and numerical Lagrangian models is needed for estimating heat and water vapor exchange, thereby increasing the suite of models for computing the canopy microenvironment.

Most steady-state leaf-scale models for stomatal conductance are rooted in empiricism. These models must be advanced on two fronts. One class of models needs to include interactive effects of controlling abiotic and biotic variables. Other models must be developed that are fundamentally mechanistic.

Dynamic induction and adaptive effects on stomatal conductance have been observed in the field and laboratory (Chazdon and Pearcy, 1986; Kirschbaum et al., 1988). Dynamic stomatal conductance models must be developed further so these processes can be extrapolated to the stand level and tested against canopy flux measurements. Additional studies on the temporal and spatial structure of the light regime in canopies will be required to make this extension. Also needed are more data on the three-dimensional distribution of foliage elements and the further development of canopy radiative transfer models that can be used to scale dynamic effects of sunflecks on leaves to the canopy level.

The role of soil moisture needs further study. Recent studies suggest that stomatal action operates independently of leaf water potential (Gollan et al., 1986). However, the generality of this response among vegetation classes has yet to be evaluated. Models also need to be developed that incorporate the effects of soil moisture and induced hormonal signals on stomatal conductance.

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