

Stomatal Control of Transpiration: Scaling Up from Leaf to Region

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I. INTRODUCTION

The study of leaf anatomy and of the mechanisms of the opening and closing of stomatal guard cells leads one to suppose that the stomata constitute the main or even the sole regulating system in leaf transpiration.

G. G. J. BANGE, 1953

evapotranspiration is independent of the character of the plant cover, of soil type and of land utilization to the extent that it varies under normal conditions.

C. W. THORNTHWAITE, in Wilm, 1944

It is widely supposed by plant physiologists and ecologists that stomata play a dominant role in regulating the amount of water transpired by vegetation. Theoretical studies on diffusion through single pores (Brown and Escombe, 1900; Milthorpe and Penman, 1967; Parlange and Waggoner, 1970) and a multitude of studies on single leaves in the leaf cham-

ber and in the field support this view (e.g., Schulze *et al.*, 1972; Burrows and Milthorpe, 1976). Yet the view is not universally accepted by micrometeorologists who tend to emphasise the large amount of energy needed to evaporate water and stress the control exerted by the supply of this energy. With this in mind, meteorologists have developed a wide variety of formulae for estimating evaporation from vegetation (e.g., Thornthwaite, 1948; Penman, 1948; Turc, 1954; Priestley and Taylor, 1972) that are based entirely on weather variables and take no account at all of the species composition or stomatal properties of the transpiring vegetation. These "potential evaporation" formulae are widely and, to a large degree, successfully used for estimating evaporation from vegetation that is not water-stressed. Clearly we have a conflict here, and one that demands resolution, since, as we shall show, each group has drawn reasonable conclusions from its experiments.

In this article we shall discuss why the conflict has arisen and how the two views can be reconciled. To do this in a systematic way we must ask most precisely the question, "To what extent do stomata control transpiration?" Our approach will be through the equivalent question, "What will be the total change in transpiration, dE , due to a small, autonomous change in stomatal conductance, dg_s ?"

In a general way we know that transpiration depends on stomatal conductance (g_s), net radiation receipt (R_n), and upon air saturation deficit (D), temperature (T) and wind speed (u). We also know that saturation deficit and wind speed vary through leaf boundary layers, through canopies and through the atmosphere above the canopies, so that it matters where they are measured. However, if we can agree on a suitable reference level for their measurement, a general statement of the dependence of transpiration on these variables can be written as¹

$$E = E(g_s, R_n, D, T, u) \quad (1)$$

We can then write a general expression for dE using the formal rules of differential calculus, of the form

$$dE = \frac{(\delta E)}{(\delta g_s)} dg_s + \frac{(\delta E)}{(\delta D)} dD + \frac{(\delta E)}{(\delta R_n)} dR_n + \frac{(\delta E)}{(\delta T)} dT + \frac{(\delta E)}{(\delta u)} du \quad (2)$$

This states that we must consider not only the primary sensitivity of a change in transpiration, dE , to stomatal changes, dg_s , but also take note of the sensitivity of transpiration to the consequential changes in saturation deficit, net radiation, temperature and wind speed. For simplicity we shall neglect the effects of changed evaporation rates and energy balances on net radiation, temperature and wind speed and set dR_n , dT and du

¹ Symbols for quantities are listed and defined in Appendix B.

equal to zero: We shall focus particularly on the response of the saturation deficits, dD , to a change in stomatal conductance and on the importance of this to changes in transpiration, dE .

The sensitivity of saturation deficit to changes in stomatal conductance depends on where the saturation deficit is measured. If all of the stomata on a single leaf change aperture in unison, there may be a substantial change in saturation deficit measured at the leaf surface, but a negligible change in saturation deficit measured a centimeter or two away, outside the leaf boundary layer. Two different values of dD may be obtained in this simple case, depending on the place where dD is measured. Since the change in evaporation does not depend on from where we observe it, it seems that we are free to choose a convenient observation point. In this discussion a reference location will always be chosen far enough away from the site of evaporation that $dD = 0$, so that we may write

$$dE = \frac{(\delta E)}{\delta g_s} dg_s \quad (3)$$

But this raises difficulties. Where should a reference be located if D is not to change significantly? The answer must depend on the scale of the area over which the stomatal conductance changes. If the aperture of only a single stomatal pore alters, then the saturation deficit adjacent to that pore would scarcely be altered, but if all the stomata of all the leaves in an extended canopy change, then the effects on the saturation deficit would be felt throughout the whole of the turbulent planetary boundary layer up to perhaps 1000 m or more. Only the conditions above the planetary boundary layer, which are set by the larger scale circulation of the atmosphere, would be unaffected.

This question of scale is the central issue addressed in this essay. As the scale of change of stomatal conductance increases, a suitable observational reference (where $dD = 0$) must be located further and further away from the surface, and more and more local adjustment of D will take place near the surface. To begin our analysis, we first survey the historical developments that have led "physiologists" to conclude that transpiration is strongly regulated by stomata and "meteorologists" to conclude that it is not. We note at the outset that the scale of the experimental systems studied by these two groups is quite different.

II. ORIGIN OF THE CONFLICT

Over 250 years ago, Stephen Hales (1727) concluded from experiments on potted trees in his garden that sap flow through the stem was propor-

tional to the area of (stomatal) pores in the leaf. Through the late nineteenth and early twentieth century, plant physiologists such as Schwendener, von Sachs and Leitgeb and ecologists such as Haberlandt, Warming and Warrington deduced from experiments on leaves and plants (see von Sachs, 1887, for examples) that "Stomata . . . are adapted by their mobility and structure to regulate transpiration" (Warming, 1909). In these experiments by the early plant physiologists, transpiration was usually measured from individual leaves or plants that had been removed from their normal place in the field to artificial conditions in the laboratory. One consequence of bringing plants in from the field to the laboratory is that their leaves then become exposed to conditions of radiation, temperature and saturation deficit far removed from the conditions in the immediate environment that they would have experienced within a community in the field (von Sachs, 1887). Even when experiments were done outdoors, conditions were frequently far from natural. Stephen Hales, for example, illustrated his experiments with pictures of trees in tubs and detached branches on his patio, and in the extensive investigations of Briggs and his colleagues (e.g., Briggs and Shantz, 1916; Shantz and Piemeisel, 1927), water loss was measured from potted plants of field crops spaced out on a soil or gravel apron. Fifty years later Hudson (1965) criticised such experimental design on the grounds that wholly misleading conclusions are usually reached regarding both the rate and control of transpiration, but experiments on stomatal control of transpiration of similar design are still common today. The question arises then as to the effect this kind of exposure has on water loss and on the interpretation of stomatal control of water loss.

Although stomata were generally regarded as controlling transpiration during the first half of this century, the laboratory experiments seemed to show that control was only exercised effectively when the stomatal pores were almost closed. This view arose because the leaves of plants were often poorly ventilated and the significance of low leaf boundary-layer conductance was not appreciated. The idea persisted, by and large, until the early 1950s when re-analysis of gaseous diffusion through small pores and stomata (Penman and Schofield, 1951; Bange, 1953) and experiments on unventilated and ventilated leaves by Bange demonstrated that the effectiveness of stomatal control of transpiration increased with increasing ventilation over the full range of stomatal apertures. They showed that neglect of the large boundary layers that may develop in experiments in still air had led to an underestimation of the effectiveness of the stomata and overestimation of the likely rate of transpiration: Brown and Escombe (1900), for example, missed the significance of the leaf boundary layer and thereby overestimated transpiration severalfold. In the field,

leaf boundary-layer conductances are usually one or two orders of magnitude larger than stomatal conductances, depending upon leaf size and ventilation rate (Grace, 1977), and consequently their influence on transpiration rate is generally small. Very large leaves, such as the leaves of some tropical trees, may, however, be exceptions to this and have boundary-layer conductances that are much smaller than the stomatal conductance (e.g., Grace *et al.*, 1980).

The omission of boundary-layer conductance by the early physiologists contributed to the development and acceptance of concepts such as "atmospheric demand" and "potential evaporation", as evaporation had to be determined by the weather if the stomata exerted no control. The more recent use by physiologists of sophisticated systems for controlling the environment of leaves and plants, and of instruments for measuring transpiration and stomatal conductance, has made possible the routine demonstration in the laboratory of the dependence of transpiration on stomatal conductance: if the boundary-layer conductance is large relative to the stomatal conductance, the transpiration rate is approximately proportional to the stomatal conductance (e.g., Fig. 1). But physiologists must ask whether the results obtained in these artificial circumstances are relevant in natural conditions on a field scale.

Meteorologists, on the other hand, have little reason to ask whether they are doing their experiments under natural conditions. Outdoor field experiments are, as far as they are concerned, performed in natural conditions by definition and have led to an emphasis on the weather as the most important determinant of transpiration, provided that soil water supply is not limiting. Thornthwaite (see Wilm, 1944) was the first to state the principle explicitly. He examined water use data from a number of crops and also seasonal water balance data from a number of catchments and arrived at the conclusion quoted at the beginning of this article. Penman's study of evaporation from a sunken Meteorological Office pan and grassland soon followed (1948), and his meteorological formula became widely used to estimate evaporation from vegetation.

This "weather-controlled" evaporation was not seen to be in conflict with physiological opinion, since most physiologists then believed that stomatal control of transpiration was effective only when the stomata were nearly closed. Good correlations between field evaporation rates and the weather were interpreted as showing that physical rather than physiological variables regulated transpiration: Throughout most of the range of soil water availability plants were thought to be "wet", or to behave as passive wicks, conducting water from the soil to the atmosphere without exercising significant control (e.g., Van Bavel *et al.*, 1963; Fritschen and Van Bavel, 1964).

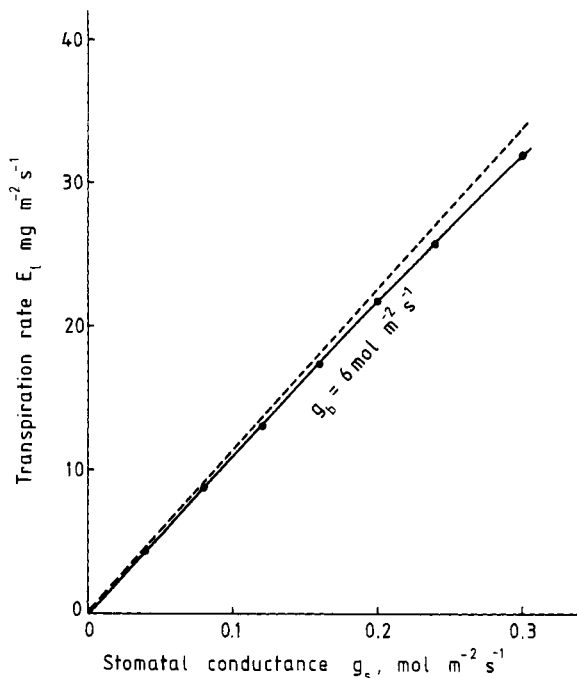


Fig. 1. The relationship between transpiration rate and stomatal conductance of a Sitka spruce shoot measured in a well-stirred cuvette with a constant saturation deficit of 6 millibars at 20°C. The dashed line is the line of zero leaf boundary layer resistance.

Penman and Schofield (1951) included stomatal resistance in their calculations of transpiration from crops, but substantially underestimated the significance of the stomata. Because suitable values for the aerodynamic transport resistances of the air layers above the crop were not available, they took values appropriate to the very smooth water surface determined earlier for the Meteorological Office pan (Penman, 1948). Thus, the aerodynamic resistance was overestimated and, as a result, the significance of stomatal conductance was largely missed.

Until 1963, the idea of "wet" plants prevailed and many weather-based or "potential evaporation" formulae were developed and tested. However, by 1966 a series of papers had been published that changed the picture substantially. Monteith (1963) took up Businger's suggestion (Businger, 1956) and calculated aerodynamic resistance from wind profile theory rather than from Penman's (1948) wind function and found from field data that the aerodynamic resistance was small relative to the canopy resistance of a bean crop. Later, Monteith *et al.* (1965) demonstrated

comprehensively that the canopy resistance of an actively growing barley crop was not insignificant compared to the aerodynamic resistance, and Van Bavel (1966) showed conclusively that aerodynamic resistances should be calculated according to wind profile theory.

This left meteorologists in a dilemma and two lines of research developed. On the one hand, some researchers proceeded to explore the new idea of canopy resistance (Monteith, 1965; Van Bavel and Ehrler, 1968; Black *et al.*, 1970), while others continued in the search for better ways to estimate potential evaporation (Morton, 1968; Priestley and Taylor, 1972). To illustrate the power of this latter trend, we give an example of the empirical relationship between daily evaporation from three crops grown in two different regional climates in New Zealand and the Priestley and Taylor estimates of transpiration based solely on net radiation and temperature (Fig. 2).

The meteorological argument emphasising energy control of transpiration is based on recognition that evaporation requires a large amount of energy and on empirical correlations that “explain” (in the statistical sense) most of the variance of evaporation in many experiments. Engineering practice almost universally employs the concept of weather-only-controlled transpiration, and equations such as those of Penman and of Priestley and Taylor are widely used.

To summarise these two different lines of research on transpiration, one by physiologists and the other by meteorologists, we may state that

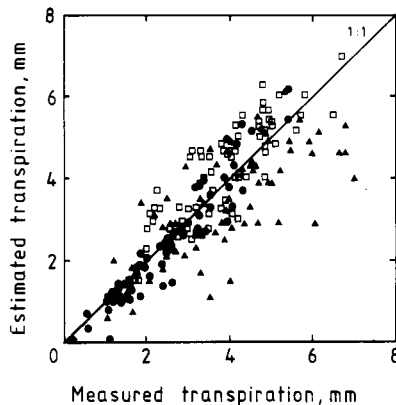


Fig. 2. A comparison between daily transpiration estimated by the Priestley and Taylor (1972) equation (i.e., as $1.26 E_{eq}$) and measured by the Bowen ratio/energy balance method for three crops at two geographically different locations in New Zealand: (●), Oats, Palmerston North; (▲), barley, Lincoln; (□), pasture, Palmerston North. After McNaughton *et al.* (1983).

physiological experience has mostly been gained from experiments in the laboratory on single leaves or plants in environmental conditions that are independently controlled, or at least "unnatural". Meteorological knowledge has, on the other hand, been gained in the field with large numbers of plants covering areas of a hectare or more exposed to an uncontrolled environment that we must suppose reflects the weather and surrounding vegetation on a larger scale.

III. A QUESTION OF SCALES

In the following sections we analyse the question of scale in more detail. We shall begin by discussing stomatal control of transpiration at the finest possible scale, where the change occurs in only a single stomatal pore, and move to progressively larger scales in subsequent sections.

A. The Single Stoma

Following Brown and Escombe (1900), we consider a model of the transfer of water vapour through an individual stoma (Fig. 3). Water

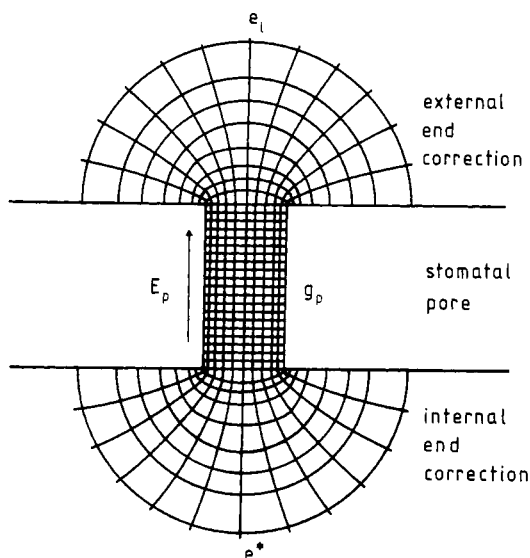


Fig. 3. A diagram to show the path of water vapour through a single stomatal pore, showing the converging and diverging lines of flow that delimit volumes of equal vapour density. After Brown and Escombe (1900).

evaporates at the surface of the cell walls around the substomatal cavity, especially those closest to the pore itself (Tyree and Yianoulis, 1980), and moves by diffusive and viscous flow (Leuning, 1983) through the pore. The source of water vapour is air, saturated with water at the appropriate local cell wall temperature and with water vapour pressure e^* . For a single stoma, the sink for water vapour is the ambient air, with vapour pressure e_l just beyond the mouth of the pore at the limit of influence of the end effect of the pore. This is effectively at the surface of the leaf. The flux of water through the pore (E_p) is

$$E_p = g_p(e^* - e_l)/P \quad (4a)$$

where

$$g_p \approx aP\mathcal{D}_w/(lRT) \quad (4b)$$

If E_p is in units of mol sec^{-1} per pore and e and P are vapour pressure and atmospheric pressure in consistent units of pressure, g_p also has units of mol sec^{-1} per pore. [The partial water vapour pressures normalised with respect to atmospheric pressure in Eq. (4a) are identical to mole fractions.] The diffusivity of water in air, \mathcal{D}_w , in Eq. (4b) is a complex quantity embracing both true diffusion and viscous flow through the pore of depth, l , and area, a , and depends on the total pressure, the other gases present and the pore size (Leuning, 1983). The source vapour pressure is taken as equal to the saturated vapour pressure at the appropriate leaf temperature, since the thermodynamic relationship between water potential, ψ , and relative humidity, e/e^* ,

$$\psi = \ln(e/e^*)RT/\bar{V}_w \quad (5)$$

can be used to show that even if the water potential in the cell wall was as low as -4 MPa (Jarvis and Slatyer, 1970), e would still be 0.97 of e^* (see table of values in Milthorpe, 1962).

Leaf cells have a high water content and consequently a high thermal conductance. For an isothermal system around the stoma, Eq. (4) can be written as

$$E_p = g_p D_e / P \quad (6)$$

where D_e is the saturation deficit at the effective surface of the leaf. It is particularly useful to use saturation deficit in this context rather than partial pressure or amount of water vapour because saturation deficit takes into account changes in temperature that result from changes in the energy balance at the surface.

For a single pore, we can assume that the saturation deficit at the leaf surface, D_e , does not depend on the transpiration through the pore, E_p ,

because the contribution of transpiration through a single pore has an infinitesimal effect on the conditions near the leaf surface. Thus, D_ℓ can be regarded as independent of both g_p and E_p . Then differentiating Eq. (6) leads to

$$dE_p/E_p = dg_p/g_p \quad (7)$$

This equation states that a fractional change in conductance of a single pore acting alone leads to an equal fractional change in transpiration through that pore. Thus, at the level of a single stoma, transpiration is perfectly controlled by pore geometry and hence is perfectly regulated by the movements of the guard cells. This is a significant deduction for a single pore, and we must next ask the question whether it is also true for a population of pores when the conductances of many pores change in unison.

Brown and Escombe (1900) tried unsuccessfully to extrapolate from the properties of an individual stoma to the evaporation of water from an entire leaf, but failed to recognise that there is an important distinction between the flux of water through a single stoma and that through a population of stomatal pores. If the aperture of a single stomatal pore changes, the resulting change in vapour flux through that pore can cause only an infinitesimal change to the saturation deficit above the neighboring stomatal pores. If, on the other hand, the apertures of very many of the pores change, their joint effect is to alter significantly the saturation deficit near the leaf surface. In the arguments leading to Eq. (6) for a single pore, we assumed that D_ℓ was independent of E_p , but we must now revise this assumption when systematic changes in pore dimensions occur over the surface of a leaf so that the average stomatal conductance changes.

B. The Single Leaf

Our analysis here will treat the leaf as an idealised flat lamina, uniform with respect to both stomatal behaviour and transport processes through the air layer adjacent to the leaf. Thus, if there are n stomatal pores per unit area of leaf surface, the conductance of the population of pores per unit surface area of leaf is

$$g_s = \sum_{i=1}^n g_{p,i} \quad (8)$$

and the flux density of water through the pores on that leaf surface (per unit surface area of leaf) is

$$E_\ell = g_s D_\ell / P \quad (9)$$

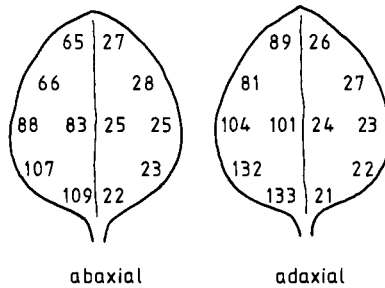


Fig. 4. The variation in average stomatal density (left halves, number per mm²) and stomatal pore lengths (right halves, μm) over the abaxial and adaxial surface of tobacco leaves. After Slavik (1963).

But before accepting this idealised view, we should first look at the complexity of real leaves and appreciate the approximations that must be made to model transpiration at even this modest level of spatial integration.

Figure 4 shows the variation of stomatal density and pore length over a single leaf of tobacco as measured by Slavik (1963). The stomatal densities almost double from the tip to the base while stomatal lengths decrease by about one-quarter in the same direction. In this case, changes of dimensions from base to tip are coordinated so that the conductance of fully open stomata is likely to be similar along the leaf, but this cannot be expected in general. Usually differences in illumination will occur along a leaf because of variations in both shading by other leaves in a canopy and in orientation of parts of an irregularly shaped leaf with respect to the solar beam. Water potential gradients will also occur as a result of internal resistances to water movement through the leaf (Tyree and Yianoulis, 1980), and variations in the solute potentials of guard cells may be found (Stålfelt, 1963).

The air layer over a leaf may also have variable properties. Figure 5 shows measured profiles of air speed and turbulence intensity close to the surface of a poplar leaf. Variations such as these influence the efficiency of local heat transport and can cause large variations in temperature and humidity at the leaf surface. To illustrate this, Fig. 6 shows the distribution of surface temperature over a heated runner bean leaf: Warmer parts of the leaf occur where local heat transport is least efficient.

Overall, this picture of a leaf is one of great complexity, with stomatal characteristics, illumination, water potential and local heat transport coefficients all varying strongly and possibly in a co-ordinated fashion, with the likelihood that local stomatal conductances will respond to local conditions on the leaf (Lange *et al.*, 1971). For example, Laisk *et al.* (1980) found a wide variation of stomatal conductances within small areas of

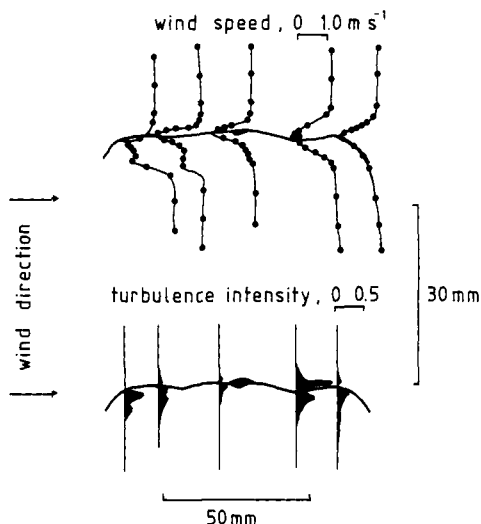


Fig. 5. Profiles of wind speed (above) and turbulence intensity (below) around a poplar leaf shown in transverse section in a laminar airstream. After Grace and Wilson (1976).

surface of barley and horsebean leaves and were able to represent the frequency distributions of these conductances by normal distributions.

Having pointed out these difficulties, we are scarcely in a position to take proper account of them in our discussion. Here we follow the common practice of plant physiologists and represent the local variation in stomatal conductance by a single average leaf conductance, the saturation deficit at the leaf surface by a single average value, and transport from the leaf surface to the atmosphere as a single average boundary-layer conductance (Penman and Schofield, 1951; Monteith, 1965). A schematic representation of our basic leaf model is shown in Fig. 7.

The saturation deficit of the ambient air, D_a , is defined outside the leaf boundary layer where its value is assumed to be independent of any change in transpiration from that individual leaf. Of course, D_a could change as a result of events external to the leaf, such as a change in the weather, an adjustment to the controls of a cuvette enclosing the leaf, or a change in transpiration by many leaves in a canopy surrounding the individual leaf. Here we are interested only in the change in transpiration from a particular, individual leaf as a result of an autonomous change in stomatal conductance of that leaf, so D_a may be considered as an externally set parameter.

Transpiration from the leaf is correctly described by Eq. (9), but, in contrast to the single pore, D_e can now no longer be regarded as indepen-

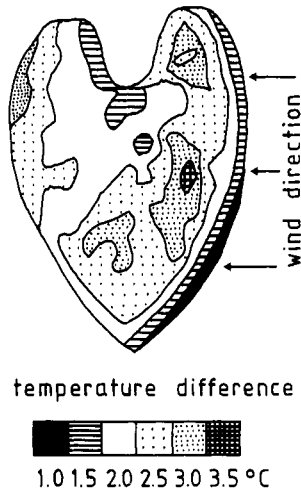


Fig. 6. A map of the distribution of temperature over the surface of a runner bean leaflet in an airstream. The scale shows the elevation of leaf temperature above air temperature. After Wigley and Clark (1974).

dent of g_s . A change in g_s of the entire leaf will cause a change in the transpiration rate which, in turn, will cause a change in the water vapour gradient across the leaf boundary layer.

At the leaf surface, energy must be conserved according to the equation

$$H + \lambda E_\ell = R_n \quad (10)$$

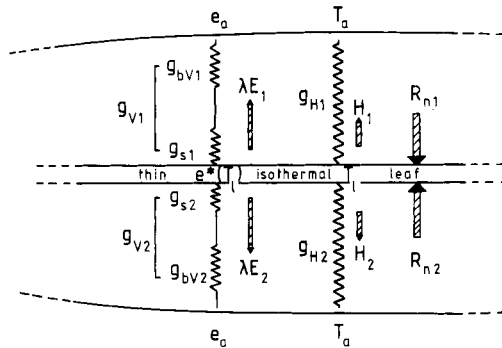


Fig. 7. A schematic representation of idealised stomatal, g_s , and boundary layer, g_b , conductances on the two sides of a symmetrical leaf in an airstream. g_v and g_H are the total conductances to water vapour and heat, respectively, between the leaf and an independent reference in the free airstream, along the gradients defined by e and T . H , λE_ℓ and R_n are the fluxes of sensible heat, water vapour and net radiation, respectively.

where H is the sensible heat flux from both sides of the leaf per unit plan area, λE_ℓ is the latent heat flux associated with the transpiration rate E_ℓ , and R_n is the net flux of radiation absorbed by both sides of the leaf per unit plan area. To conform with the convention that we have adopted of expressing fluxes and conductances in units of $\text{mol m}^{-2} \text{sec}^{-1}$, λ is the molar latent heat of vaporisation in units of J mol^{-1} (see Appendix B). Hence, a change in transpiration rate implies a change in the sensible heat flux also, and thus a change in the temperature gradient across the leaf boundary layer. As a result, an increase in g_s will cause an increase in vapour pressure and a decrease in temperature at the leaf surface and so lead to a decrease in D_ℓ . The resulting increment in transpiration will be somewhat less than would have obtained had D_ℓ been held constant.

To describe these effects, we develop an equation equivalent to the Penman–Monteith equation in Appendix A and write equations for D_ℓ and E_ℓ as

$$D_\ell = \Omega_\ell D_{\text{eq}} + (1 - \Omega_\ell) D_a \quad (11)$$

and

$$E_\ell = \Omega_\ell E_{\text{eq}} + (1 - \Omega_\ell) E_{\text{imp}} \quad (12)$$

where Ω_ℓ , D_{eq} , E_{eq} , and E_{imp} are defined by expressions in Appendix A. We also obtain an expression for the sensitivity of a change in transpiration by a leaf to a fractional change in stomatal conductance of that leaf as

$$dE_\ell/E_\ell = (1 - \Omega_\ell) dg_s/g_s \quad (13)$$

These relationships apply equally to hypostomatous leaves and to symmetrical amphistomatous leaves, although the exact definition of Ω_ℓ is somewhat different in the two cases. Equation (13) is most important to our argument, so it is important to have a qualitative understanding of the meaning of Ω_ℓ and an indication of the range of numerical values that it may take.

We may regard Ω_ℓ as a decoupling factor that describes how closely the saturation deficit at the leaf surface is linked to that of the air outside the leaf boundary layer. It is a dimensionless factor that assumes values in the range 0 to 1, depending on the sizes of the boundary layer and stomatal conductances, g_b and g_s , of the two leaf surfaces and temperature, insofar as ϵ depends on temperature as defined by Eqs. (A16) and (A21). The leaf boundary-layer conductances are involved because they influence the gradients of saturation deficit close to the leaf. Large boundary-layer conductances usually mean small gradients of D through the boundary layers and hence strong coupling between D_ℓ and D_a . The stomatal conductances also determine the degree of coupling, but in a less obvious

way. Large stomatal conductances minimise the gradients of D through the stomata, so that D_ℓ tends towards zero. To take an extreme situation, if the surfaces of the leaf are wet (i.e., $g_s \rightarrow \infty$), D_ℓ becomes zero and remains so irrespective of any changes in evaporation rate caused by changes in D_a or g_b . Thus, D_ℓ is decoupled from D_a and $\Omega_\ell = 1$. At smaller values of g_s , D_ℓ changes in response to changes in transpiration rate caused by changes in D_a or g_b , and the result is that coupling between D_ℓ and D_a increases as g_s decreases.

At the lower limit of $\Omega_\ell = 0$, the coupling is very strong and the saturation deficit at the leaf surface is equal to that in the air outside the leaf boundary layer. Then the vapour and heat fluxes from the leaf surface do not cause a general change in saturation deficit at the leaf surface. With D_ℓ equal to the externally set value D_a , a fractional change in stomatal conductance would cause an equal fractional change in transpiration, as was the case for the single pore. We call the transpiration rate when $D_\ell = D_a$ the imposed transpiration rate, E_{imp} .

At the other extreme, when $\Omega_\ell = 1.0$, conditions at the leaf surface are completely decoupled from conditions in the air outside the leaf boundary layer, and D_ℓ tends toward a local equilibrium value, D_{eq} . This equilibrium value of the saturation deficit depends principally on net radiation receipt and the stomatal conductance itself, in such a way that the equilibrium transpiration rate, E_{eq} in Eq. (12), is independent of stomatal conductance. Then, as Eq. (13) shows, a fractional change in stomatal conductance will cause a decreasing fractional change in transpiration rate of the leaf as Ω_ℓ approaches 1.0. At this extreme a small change in stomatal conductance over the whole leaf will not cause any change in transpiration rate, so the stomata do not control transpiration from the leaf as a whole.

Nonetheless, even when $\Omega_\ell = 1$ for the whole leaf, the water vapour flux through *individual* stomatal pores remains under the control of the individual pairs of guard cells. For a leaf completely decoupled from its external environment, the saturation deficit at the surface, D_ℓ , equilibrates to a value principally defined by net radiation receipt and mean conductance per unit leaf surface area of all of the stomatal pores over the leaf surface. Were the mean stomatal conductance of all the pores to change, there would be a change in D_ℓ , but no change in E_ℓ . Were the conductance of a single pore to change, there would be an increase in transpiration through that pore, an infinitesimal effect on both D_ℓ and the mean stomatal conductance, and no change in E_ℓ from the whole leaf. From the point of view of the individual pore, D_ℓ remains essentially constant and the fractional change in transpiration through that pore equals the fractional change in stomatal conductance of that pore, in accord with Eq. (7). There is no contradiction between a lack of stomatal

control of transpiration at the level of the whole leaf and perfect stomatal control of transpiration through an individual pore.

At intermediate values of Ω_ℓ , intermediate degrees of stomatal control prevail and E_ℓ depends jointly on the net radiation received, on external conditions of D_a and windspeed and on the stomatal conductance. This is illustrated diagrammatically in Fig. 8. In this figure, the equilibrium rate of transpiration, as determined by net radiation, temperature and the ratio of boundary-layer conductances of the two leaf surfaces, is shown on the left-hand ordinate corresponding to $\Omega_\ell = 1$. As Ω_ℓ goes from 1 to 0, this component falls and the contribution by E_{imp} increases. Three examples of E_{imp} are shown on the right-hand ordinate, representing three different combinations of the air saturation deficit and leaf stomatal conductance. Depending on the size of $g_s D_a$, the total transpiration rate at any value of Ω_ℓ may be similar to the equilibrium rate ($E_{\ell 2}$) or lie above it ($E_{\ell 1}$) or below it ($E_{\ell 3}$). That the rate of transpiration happens to coincide with the calculated equilibrium rate cannot be taken as evidence that $\Omega_\ell = 1$.

Table 1 gives some values for Ω_ℓ calculated for leaves for which published values for g_s and g_b are available. Boundary-layer conductances appropriate for ventilation rates of 0.2, 1.0 and 5.0 m sec⁻¹ were used.

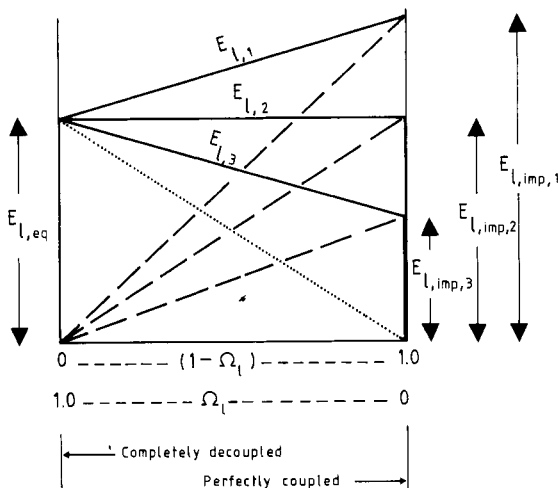


Fig. 8. A diagram to show the effect of changing coupling between leaf and air on the relative proportions of equilibrium and imposed transpiration making up the total transpiration from a leaf. An equilibrium rate, set by net radiation receipt and air temperature, is assumed on the left-hand ordinate and combined with three alternative examples of imposed rates, set by air saturation deficit and stomatal conductance, on the right-hand ordinate, as Ω_ℓ changes from 1.0 to 0. (---), contribution of equilibrium evaporation; (---), contribution of imposed evaporation; (—), total evaporation.

Table 1
Values of Ω_t for Isolated, Individual, Hypostomatous Leaves of Several Species Varying in Leaf Size (d) and
Maximal Stomatal Conductance (g_s)^a

Species	g_s (mol m ⁻² sec ⁻¹)	d (mm)	ε	Ω_t			Source of data
				u (m sec ⁻¹)			
				0.2	1.0	5.0	
<i>Tectonia grandis</i> (teak)	1.10	260	4	0.97	0.94	0.79	
(Dry or wet season)	1.41	260	3	0.97	0.95	0.80	Grace <i>et al.</i> (1980)
<i>Gmelina arborea</i>	0.55	140	4	0.95	0.85	0.63	Whitehead <i>et al.</i> (1981)
(Dry or wet season)	1.00	140	3	0.97	0.89	0.71	Grace <i>et al.</i> (1982)
<i>Triplochiton scleroxylon</i>	0.28	200	3	0.80	0.64	0.35	Ladipo <i>et al.</i> (1984)
<i>Malus pumila</i> cv. Golden Delicious	0.21	60	2	0.50	0.26	0.11	Landsberg and Powell (1973)
(Extension or spur leaves)	0.41	60	2	0.67	0.41	0.19	Warritt <i>et al.</i> (1980)
<i>Fagus sylvatica</i> (beech)	0.10	40	2	0.50	0.23	0.10	Dixon (1982)
<i>Picea sitchensis</i> (Stika spruce)	0.34	2	2	0.46	0.25	0.12	Landsberg and Thom (1971)
(Current, 1- or 3-year-old leaves)	0.07	2	2	0.18	0.08	0.03	Jarvis <i>et al.</i> (1976)
	0.03	2	2	0.07	0.03	0.01	

^a Ω_t was calculated from Eq. (A21) assuming $g_{b1} = g_{b2} = g_b$ with ε taken as 2 (18°C), 3 (26°C) or 4 (32°C). Values of g_b were read from curves or calculated from functions relating g_b to the free stream windspeed in conditions of forced convection and net radiation close to zero. Sitka spruce is not strictly hypostomatous, but the majority of the stomata are in one surface.

These conditions may be taken to be typical of windspeeds indoors in a laboratory or a glasshouse (0.2 m sec^{-1}), indoors in a well-ventilated cuvette or outdoors in a low canopy or at the base of a tall canopy (1 m sec^{-1}), or outdoors near the top of a tall canopy (5 m sec^{-1}). For want of any better information, the boundary-layer conductances are assumed equal for the two surfaces of hypostomatous leaves.

Values of Ω_ℓ vary from close to 1.0 for the large leaves of teak to close to zero for the small leaves of conifers. Values of Ω_ℓ also decrease with increasing windspeed. Figure 9, from Bange (1953), shows the change in transpiration rate with respect to stomatal aperture in *Zebrina pendula*. At maximum stomatal opening, values of Ω_ℓ in still air and moving air were, respectively, 0.7 and 0.2. For similar boundary-layer conductances, values of Ω_ℓ are smaller for hypostomatous leaves than for amphistomatous leaves. A consequence of this is that transpiration from hypostomatous leaves is more sensitively controlled by changes in g_s than is transpiration from amphistomatous leaves. This may possibly relate to the frequent occurrence of hypostomatous leaves on tall trees.

In summary, at the leaf scale, stomatal control of transpiration can be either large or small, depending on how well the saturation deficit at the leaf surface is coupled to that of the ambient air. This coupling is usually very strong for small well-ventilated leaves. In general, the degree of

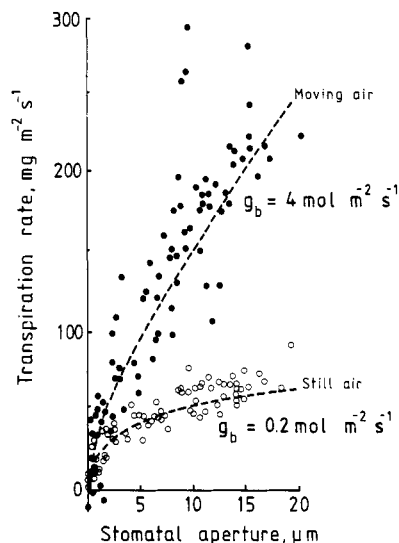


Fig. 9. The influence of stomatal aperture on transpiration of *Zebrina pendula* leaves in moving and still air. The dashed lines show the response predicted from diffusion theory. After Bange (1953).

sensitivity of transpiration from a single leaf to changes in conductance of that leaf varies according to exposure to wind and so can vary according to whether the leaf is located in a glasshouse, in a leaf chamber or out in the field.

C. The Individual Plant

An isolated leaf might be found, for example, in a cuvette or on a seedling. However, a leaf is commonly a part of the population of leaves on a plant. As air moves through the crown of a single plant, heat and water vapour will be added to the airstream, but the effect of this on the saturation deficit around the leaves will be very small indeed (Rose, 1984). Essentially, D_a is determined by the vegetation and weather upwind of the plant and is uninfluenced by transpiration from the plant itself. Thus, we can continue to use Eq. (13) with g_s and g_b as previously defined to calculate the effect of a fractional change in stomatal conductance on transpiration. If the stomatal conductance of one particular leaf, or indeed in this case of all the leaves, on the plant changes fractionally, the consequent fractional change in transpiration depends on the size of Ω_ℓ calculated for the individual leaves.

Leaves on a plant are often grouped together around the shoot axes, sometimes in dense clusters within which they may touch one another and their individual boundary layers may overlap. Although the saturation deficit within the clusters will depend on the transpiration rate of the leaves, the saturation deficit of the air around the leaf cluster as a whole can still be regarded as an independent variable, to all intents and purposes uninfluenced by the transpiration from the cluster of leaves. Thus, Eq. (13) may still be used to calculate the effect of a fractional change in stomatal conductance on transpiration, but we now need to take into account the rather smaller boundary-layer conductances associated with transport from the cluster as a whole. The value of Ω_ℓ for the cluster will be larger than for a single leaf exposed alone in the same airstream. Equations describing the effects of grouping together of leaves on g_b of individual leaves of spruce and apple (Landsberg and Thom, 1971; Landsberg and Powell, 1973) indicate that grouping can decrease values of g_b by 50% at windspeeds in the range of 1 to 2 m sec⁻¹, and this leads to larger values of Ω_ℓ for clusters of leaves than for individual leaves. In this case then, a fractional change in stomatal conductance will have a somewhat smaller effect on transpiration than in the case of the isolated individual leaf.

When many individual plants are grouped together into a larger clump or thicket, we can no longer assume that the saturation deficit of the air

passing through the canopy is independent of a change in the average stomatal conductance of the assemblage of plants. The resulting changes in heat and water vapour fluxes from the transpiring leaves into the air moving through the canopy space may be sufficient to change the saturation deficit of that air significantly. Whilst a fractional change in the stomatal conductance of any one leaf acting alone will lead to a change in the transpiration rate of that leaf, it will have no significant effect on the saturation deficit around the leaves. However, this will no longer be true if the stomatal conductances of all the leaves in the canopy change together. In this case D_a will change with the transpiration rate so that we can no longer regard D_a as an externally set variable. As the scale of the stomatal conductance increases from a single leaf or plant to an extended canopy, we must move our reference location for saturation deficit up into the atmosphere above the canopy to a new level where it is again independent of changes in stomatal conductance.

D. The Extensive Canopy

We turn now to consider the effect on transpiration of a change in the average stomatal conductance of all the leaves in a field or forest stand. In this case, the effects of changes in the fluxes of heat and water vapour from all the individual leaves are likely to accumulate and lead to substantial changes in the saturation deficit around the leaves throughout the canopy.

To calculate the effect of a fractional change in average stomatal conductance on transpiration by the canopy, we must predict the resultant changes in saturation deficit that will occur both within and above the canopy as a result of the changes in stomatal conductance. These changes in saturation deficits will reflect both the changed fluxes of heat and water vapour at the surfaces and the larger scale meteorological situation.

This situation may be analysed in an analogous way to our treatment of the leaf if we can define an effective canopy conductance and an effective surface saturation deficit. The variation in stomatal conductance of the diverse leaves throughout the canopy is analogous to the variation in stomatal pore properties over the surface of a single leaf that we discussed previously, and it raises similar problems. The variation in saturation deficit that may occur with height through a canopy also raises a problem in defining a single effective surface value analogous to D_l of the individual leaf. Above the canopy, a reference level must be found where the saturation deficit is unchanging as transpiration by the entire canopy changes. This is analogous to the problem we had earlier of finding an independent saturation deficit, D_a , when scaling up from the stomatal

pore to the whole leaf. Once a canopy conductance, an effective surface saturation deficit and a reference location are all defined, we shall be in a position to discuss the effect of changes in stomatal conductance on the heat and water vapour fluxes from the average leaf surface, through the leaf and canopy boundary layers to an effective sink for heat and water vapour above the canopy.

First we consider the definition of a canopy conductance. The stomatal conductance of leaves in a canopy can be highly variable. Stomatal conductance depends on light, temperature, carbon dioxide, saturation deficit and leaf water potential, all of which may vary with position in a canopy; g_s also depends on past environmental history, both immediate and more distant, age and physiological condition of a leaf and its position in a branching or tillering hierarchy; g_s also varies between species and amongst individuals of the same species (e.g., Burrows and Milthorpe, 1976; Elias, 1979; Squire and Black, 1981; Leverenz *et al.*, 1982; Solarova and Pospisilova, 1983). Figure 10 illustrates the variation of g_s with height that is found in many different canopies.

To describe the canopy in terms of a single canopy conductance, we must find an appropriate total of the conductances of all the leaves in the whole canopy. The saturation deficit at the surfaces of the various leaves will usually vary systematically down through the canopy, so that leaves with equal conductances do not necessarily contribute equal amounts to canopy transpiration. In forming a total canopy conductance it would be appropriate to weight most heavily those leaves in the driest microenvironments that contribute most to canopy transpiration. Equation (A8) in Appendix A shows that transpiration from a single leaf depends on absorbed radiation, boundary layer conductance and saturation deficit in the

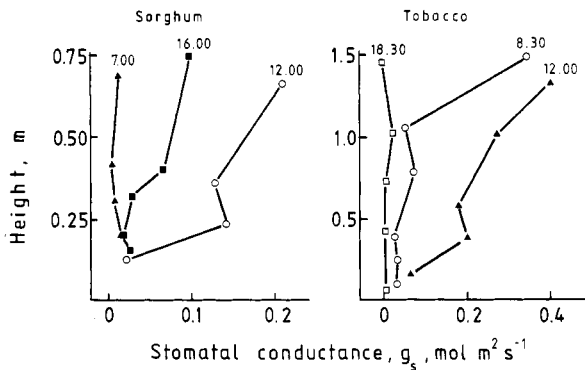


Fig. 10. The vertical distribution of abaxial stomatal conductance at three times of day in canopies of sorghum and tobacco. After Turner and Incoll (1971).

canopy space near each individual leaf. The correct weighting factors for the conductances of individual leaves can only be known if the distributions down through the canopy of these variables are also known.

In aerodynamically rough, well-ventilated canopies such as in coniferous forest, the gradients of potential temperature and humidity through the canopy are usually small, and there is little vertical gradient of saturation deficit. All leaves can then be weighted equally so that there is little difficulty in defining an average canopy conductance. This procedure is especially satisfactory when leaves are small so that leaf boundary conductances are large. Smooth canopies or very deep forest canopies may not, however, be at all well ventilated in their lower regions (Cionco, 1983; Pinker, 1983), with the result that substantial gradients of saturation deficit may develop. Figure 11 shows a difference in saturation deficit of over 2 kPa between the top and bottom of a tropical rain forest canopy. This situation may be very substantially exacerbated in canopies of large leaves tens of centimetres across, such as the leaves of teak (*Tectonia grandis*), because of the resulting large, windspeed-dependent leaf boundary layers. In such situations, the definition of a meaningful average canopy conductance becomes problematic and it may then be necessary to resort to rather more complex models that, for example, treat the canopy not as one unit, but as a series of layers.

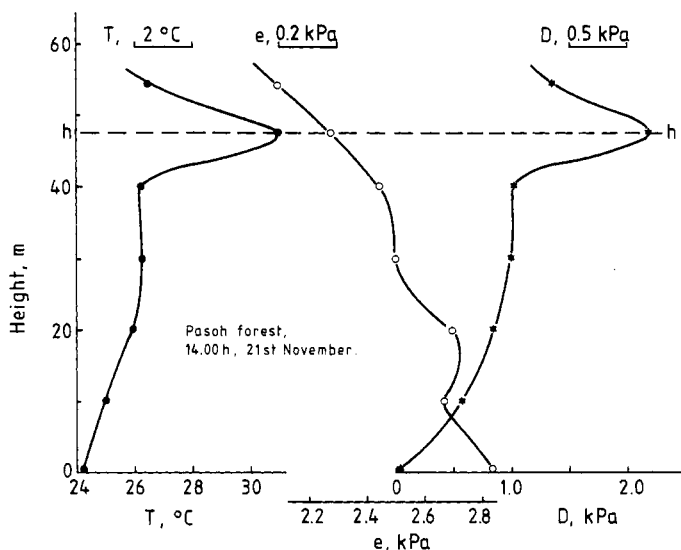


Fig. 11. Vertical profiles of air temperature (T), vapour pressure (e) and saturation deficit (D) through multistoreyed tropical forest at Pasoh Forest in Malaysia. h indicates the top of the canopy. From unpublished data of M. Aoki, K. Yabuki, and H. Koyama.

For the present discussion we follow common practice in hydrometeorology and define the canopy conductance, g_c , as the simple, unweighted total of the stomatal conductances of all of the leaves above a representative unit area of ground, and we then define the corresponding "canopy surface" saturation deficit (D_o) by the "big leaf" transpiration equation

$$E_c = g_c D_o / P \quad (14)$$

where, notionally, D_o is measured within the boundary layer of the "big leaf".

We now turn to the problem of defining a suitable reference level above the canopy. A field or forest influences the atmosphere for some distance above the canopy, so we must consider the exchange processes on a larger scale than we have done so far. We must establish a reference far enough away from the surface that the saturation deficit there is uninfluenced by any changes in the fluxes of sensible heat or water vapour at the surfaces. If the field or forest is not too large, we find this reference at the base of the well-mixed outer layer of the planetary boundary layer (PBL).

The PBL is the turbulent layer of the atmosphere extending from the ground to a height of several hundreds or thousands of metres. Within the PBL, turbulent motions facilitate vertical transport of heat and water vapour, whereas the atmosphere above is stably stratified and usually laminar, and vertical fluxes are small. The fluxes of heat and water vapour at the vegetation surface lead to gradients of potential temperature and humidity near the ground so that the saturation deficit within the vegetation canopy may deviate considerably from that above. In normal daytime (i.e., unstable) conditions we can, therefore, distinguish a surface layer comprising perhaps the lowest 50 m or so of the PBL in which appreciable gradients occur, overlain by a well-mixed outer layer within which the gradients are absent.

We consider now an area of vegetation extending from several hundred metres up to a few kilometres in a countryside that is generally vegetated for tens or hundreds of kilometres. At the upwind edge of such a field the air mass approaching has properties that are determined by the weather and the vegetation upwind. When air crosses the boundary between vegetation of one surface conductance and another, it must travel many kilometres over the new surface before complete adjustment of the vertical gradients of heat and water vapour occurs throughout the whole PBL (Burman *et al.*, 1975). However, Fig. 12 shows that substantial adjustment of the saturation deficit close to the surface may occur within a much shorter distance. Plants at the windward edge are in a similar situation to the isolated individual plants considered previously in that the saturation deficit around their leaves is imposed upon them from upwind

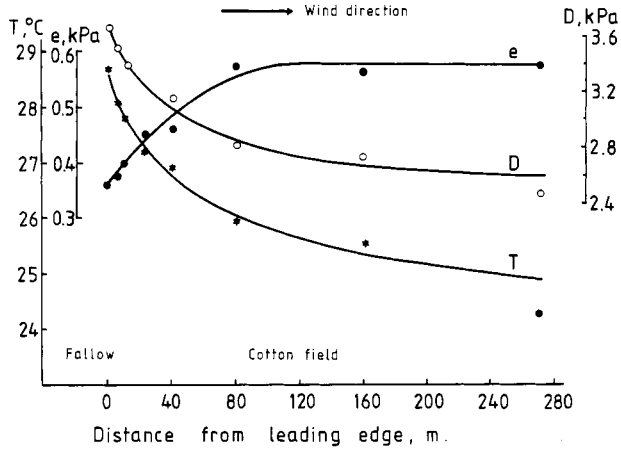


Fig. 12. Changes of vapour pressure (e), air temperature (T) and saturation deficit (D) of the air at a height of 2 m across 300 m of cotton lying downwind of dry fallow, in the Gezira. Data based on average reading over a 1-hr period on a typical day. After Davenport and Hudson (1967).

and is unaffected by the changed transpiration from the field as a whole. Consequently, a fractional change in canopy conductance of the whole area will affect transpiration from these plants at the leading edge in the same ratio as would a fractional change in the stomatal conductance of those plants standing alone [i.e., according to Eq. (13)].

Moving downwind from the edge, the internal boundary layer above the new surface grows until it comprises the whole surface layer, and the gradients of saturation deficit throughout the surface layer become well adjusted to the local fluxes of heat and water vapour. After a transitional zone of perhaps a few hundred metres we can ignore local advection at the upwind edge and use a one-dimensional model of heat and water exchange through the surface layer, analogous to the model of heat and water vapour transport through the leaf boundary layer that we have developed in detail for the single leaf. Now, however, we treat water vapour transfer from the whole canopy surface, across the surface layer to a reference within the mixed layer above, as shown in Fig. 13. We then assume that for normal convective daytime conditions, the potential saturation deficit in the mixed layer, D_m , can be regarded as a general reference value that is externally set and largely uninfluenced, at this scale of up to a few kilometres, by any changes in the surface below. For larger areas this assumption will no longer hold and D_m will adjust in response to changes in the surface fluxes of heat and water vapour, as we discuss in

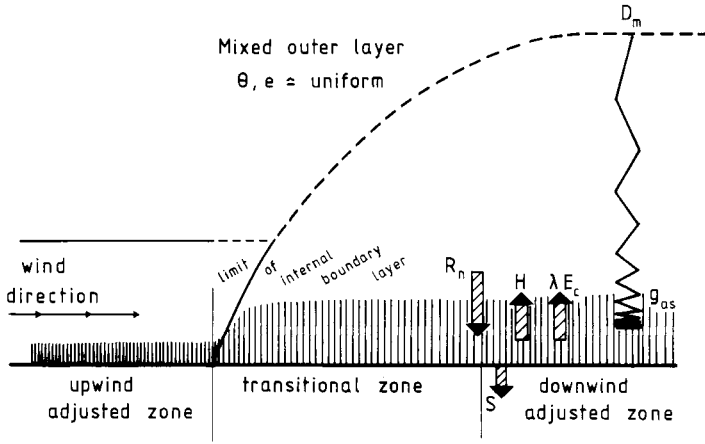


Fig. 13. A schematic representation of the total aerodynamic conductance, g_{as} , in the surface layers of the planetary boundary layer, between the vegetation surface and the base of the mixed outer layer above. H , λE_c and R_n are the fluxes of sensible heat, water vapour and net radiation, respectively. Θ and D_m are the potential temperature and potential saturation deficit in the mixed layer, respectively.

the next section. Arising from our definition of D_m , we define also an aerodynamic conductance for heat and water vapour transfer, g_{as} , across the surface layer from the effective surface of the vegetation to the reference in the mixed layer.

With these definitions we can now write the Penman–Monteith equations for the whole canopy in a form analogous to the equations for the single leaf developed earlier (McNaughton and Jarvis, 1983). Thus

$$E_c = \Omega_c E_{cq} + (1 - \Omega_c) E_{imp} \quad (15)$$

and

$$D_o = \Omega_c D_{eq} + (1 - \Omega_c) D_m \quad (16)$$

where the subscript c indicates that we are now dealing with a canopy property. The sensitivity of a change in transpiration to a fractional change in canopy conductance is again given by

$$dE_c/E_c = (1 - \Omega_c) dg_c/g_c \quad (17)$$

To answer the question of what effect a fractional change in canopy conductance will have on transpiration from the canopy, we need to know typical values of Ω_c . In Table 2 we list some values of Ω_c for different canopies. There is no difficulty in obtaining measurements of g_c for differ-

Table 2
Some Typical Values of Ω_c for Unstressed Vegetation Canopies in the Field^a

Vegetation	Ω_c	Note	Source of data
Alfalfa	0.9	b,c	Van Bavel (1967)
Permanent pasture	0.8	b,c	Russell (1980)
Grassland	0.8	a,d	McNaughton and Jarvis (1983)
Potatoes, sugar beet	0.7	b,c	Brown (1976)
Snap beans	0.7	b,c	Black (1970)
Field beans	0.6	b,c	Monteith (1963)
Barley	0.6	b,c	Russell (1980)
Wheat	0.6	b,c	Perrier <i>et al.</i> (1980)
Prairie	0.5	b,c	Ripley and Redman (1976)
Cotton	0.4	b,c	Stanhill (1976)
Heathland	0.3	a,c	Miranda <i>et al.</i> (1984)
Forest	0.2	a,d	McNaughton and Jarvis (1983)
Pine woods	0.1	a,c	Whitehead <i>et al.</i> (1984)

^a Values of Ω_c were obtained (a) from the original source, or (b) by calculation from measurements of g_s and g_{as} given in the source, with (c) g_{as} estimated up to a reference level just above the vegetation surface, or (d) up to the mixed layer.

ent kinds of vegetation, but adequate measurements of g_{as} are harder to obtain because the aerodynamic resistance of canopies is usually measured a few metres above the surface, whereas gradients of temperature and humidity persist for many tens of metres to our reference level above. We have shown previously (McNaughton and Jarvis, 1983) that about one-third of the resistance across the surface layer is located *above* the usual instrument height, depending on the windspeed, heat flux and stability. Consequently, the estimates of Ω_c in Table 2 are likely to be on the low side. Nonetheless, they show a broad range of values for crops and vegetation varying particularly in height and consequently in their aerodynamic roughness.

Putting values of Ω_c from Table 2 into Eq. (15) shows clearly that communities such as coniferous plantations are very closely coupled to the airstream overhead (Ω_c very small) and that transpiration from such communities is dominated by E_{imp} . A fractional change in canopy conductance can therefore be expected to cause an almost proportional change in transpiration. In contrast, transpiration from grassland and other smooth low vegetation (Ω_c large) is largely dominated by E_{eq} , with the consequence that a similar fractional change in g_c has very little impact on transpiration.

We must emphasise at this point that Ω_c is necessarily larger than Ω_ℓ for individual leaves of the canopy because the total conductance (boundary

layer plus surface layer) to the transfer of heat and water vapour from leaves in a canopy to an unchanging reference above the canopy is necessarily smaller than the conductance across the leaf boundary layers alone. Leaves or plants within a canopy will always be more closely coupled to the airstream within the canopy than they will be to the air in the mixed layer above the canopy, although the difference may not be large for those canopies such as coniferous forest that are exceptionally strongly coupled to the air above.

E. The Region

If a change in canopy conductance occurs in an area only a kilometre or two across, the effect of this change on the fluxes of heat and water vapour will scarcely be felt in the mixed layer of the PBL. However, if a change in canopy conductance occurs over a much larger area of perhaps several tens of kilometres across, the effect will certainly be felt throughout the mixed layer, so that D_m can no longer be regarded as independent of the resulting changes in heat and water vapour fluxes on this scale. Changes in canopy conductance over such a large area might be caused, for example, by passage of a convective storm bringing rain that alleviates extensive water stress, or by an air pollution episode causing widespread damage to leaves. Changes in land use, such as deforestation or installation of a large irrigation scheme, could also produce changes in canopy conductance on this scale, but in these cases large changes in net radiation and aerodynamic conductance of the surface layer would certainly accompany the change in canopy conductance, and these could not be ignored.

In discussing changes in transpiration on a regional scale, a different type of model must be developed. At some distance from a leaf or above a small area of vegetation, we were able to find an externally set saturation deficit and to regard the atmosphere at that distance as a sink for heat and water vapour, unaffected by any changes in the fluxes at the surface. In contrast, there is no definable sink for fluxes that affect the whole PBL; rather, heat and water vapour added at the surface accumulate within the PBL and raise its temperature and humidity. Furthermore, heat and water vapour are also added through the capping inversion at the top of the PBL as it grows by encroachment and entrainment into the stable, usually non-turbulent layers above. A model for regional transpiration must basically be a volume budget model for heat and water vapour, with particular emphasis on the processes controlling the growth in height of the PBL. Conditions above the PBL are taken, on this scale, to be independent of changes in conductance of the surface.

If the capping inversion at the top of a typical PBL is considered as an impermeable lid, then only the surface fluxes can contribute to the heat and water vapour budget of the PBL. For this case, it is readily shown that the potential saturation deficit within the PBL adjusts in such a way that equilibrium evaporation is achieved at steady state (McNaughton and Jarvis, 1983). Changes in canopy conductance lead to changes in potential saturation deficit that are sufficient to compensate completely for the original change in canopy conductance, with the result that no change in transpiration rate occurs. The stomata do not control transpiration from the vegetation as a whole in this model.

With greater realism, the top of the PBL should not be regarded as a lid but as an inversion, the base of which rises as the PBL warms from below. Mechanically and thermally produced turbulence causes mixing and entrainment into the PBL at the base of the inversion. Tennekes (1973) developed a model of this entrainment process at the top of PBL, and this has been incorporated by de Bruin (1983) into a model for regional evaporation. At the ground surface, de Bruin used the Penman-Monteith "big leaf" model for the energy exchanges, exactly as we have used it in the previous sections of this article. As an indication of the performance of the model, de Bruin (1983) expressed his calculated rates of transpiration to the equilibrium rate as a relative dimensionless ratio, α , following Priestley and Taylor (1972). In most cases the air above the PBL has a larger potential saturation deficit than the equilibrium saturation deficit, so growth in depth of the PBL leads to transpiration rates in excess of the equilibrium value except when the canopy conductance is quite small, i.e., values of α greater than one are usually expected. Results from one set of de Bruin's diurnal simulations are shown in Fig. 14. While reading this graph, it should be recalled that for most short vegetation the aerodynamic and canopy conductances are usually of similar size (Jarvis, 1981). The results of this simulation show that a 3-fold change in canopy conductance from 0.4 to 1.2 mol m⁻² sec⁻¹ can be expected to cause only about a 20% change in transpiration. An alternative formulation of a regional evaporation model (K. G. McNaughton, unpublished) takes explicit account of the potential saturation deficit above the PBL and, although it gives results that are substantially different from de Bruin's in some respects, such as rate of response of transpiration to changes in canopy conductance, it gives similar results to those shown in Fig. 14 for the dependence of α on canopy conductance.

The results from both these regional evaporation models show a rather small response of transpiration to a change in canopy conductance. The models indicate that regional evaporation is determined primarily by net radiation receipt and average temperature. This result is consistent with

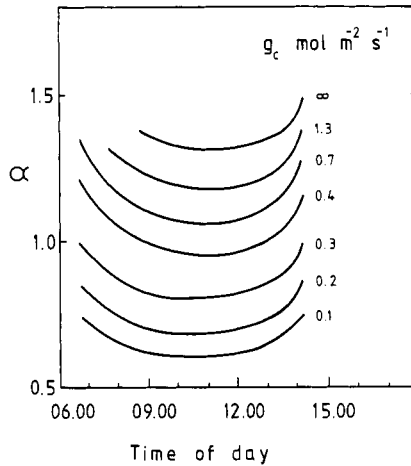


Fig. 14. Calculated regional values of the Priestley and Taylor (1972) coefficient α for different values of g_c and a constant g_{as} of $0.8 \text{ mol m}^{-2} \text{ sec}^{-1}$ (i.e., $r_{as} = 50 \text{ sec m}^{-1}$). After de Bruin (1983). Reprinted by permission of the American Meteorological Society.

the empirical results of the agricultural meteorologists and hydrologists who developed the “weather-only” interpretation of transpiration from vegetation. The most widely accepted “potential evaporation” equation, that originating in the work of Penman (1948), has as its principal component the equilibrium evaporation rate and is used to estimate transpiration from well-watered vegetation without taking account of any changes in canopy conductance. The even simpler equation of Priestley and Taylor (1972) has also proved useful: it is based only on the equilibrium evaporation rate and takes the value of α to be 1.26. Whilst Fig. 14 shows that this value of α can be expected to give acceptable estimates of regional transpiration over quite a range of values of g_c , it is clear that if the regional value of g_c were only $0.3 \text{ mol m}^{-2} \text{ sec}^{-1}$, then α should be about 0.9 rather than 1.26.

The success of these methods of estimating transpiration relies on the transpiration from the field or area of vegetation of interest being similar to the regional norm. Stanhill (1973) pointed out the difficulties in using these potential evaporation formulae to estimate transpiration from smaller areas of vegetation that are not typical of the regional environment and where D_m has not had sufficient time to adjust to the underlying surface. In these smaller scale areas, control of transpiration by canopy conductance is more important, as discussed in the previous section.

Beyond the regional scale, we might enquire about the effects of a general global change in canopy conductance. This is an important ques-

tion because one of the likely effects of rising world carbon dioxide concentration is a reduced stomatal conductance on a global scale. It should be clear from the foregoing that changes in the leaf and canopy conductance that demonstrably influence transpiration at the scale of the leaf or small field plot have progressively less influence on transpiration at the larger scales. The antitranspirant effect of carbon dioxide on leaves that is readily shown in the laboratory and glasshouse cannot be directly extrapolated to indicate a likely reduction in transpiration on the global scale, as suggested by Enoch and Hurd (1979). Almost certainly we could expect very little response of transpiration to small changes in canopy conductance, if radiation, temperature and water availability all remain constant. At the global scale, however, changes in the general atmospheric circulation are likely to accompany any change in global canopy conductance so that saturation deficits above the PBL would probably change over many regions, as would also wind direction, cloudiness and rainfall patterns, so that the overall outcome is far less certain. Significant feedback processes would probably operate, some of which might be positive and tend to increase the initial climatic effects of the perturbation. The question is unresolved at present, and this state of affairs is not helped by the fact that the general circulation models in current use do not include a description of canopy conductance in their specification of the condition of the Earth's surface.

IV. WATER STRESS

In all of the preceding discussions we have considered the consequences of only *small* changes in stomatal-pore, stomatal or canopy conductance, and we have demonstrated that the degree of stomatal control of transpiration depends, *inter alia*, upon the area scale over which changes in conductance occur. We have shown that when Ω_c is large or we deal with regional changes in canopy conductance, the sensitivity of transpiration to a change in stomatal conductance is low. Nevertheless, we know from many field observations that transpiration does indeed decline dramatically as a result of stomatal closure when soil water supply becomes limiting. In such cases, the question is not so much whether small, autonomous changes in canopy conductance can cause similar proportional changes in transpiration, but rather how much must canopy conductance change to restrict transpiration by a given amount. Very large reductions in canopy conductance will, of course, affect the assimilation of carbon dioxide adversely.

To answer this question, we can again make use of Eqs. (14) and (17),

but with E_c now the independent variable. From these equations it is apparent that a larger proportional change in canopy conductance will be necessary to bring about a given restriction of transpiration and so to maintain plant viability in the face of a reduction in the quantity of water available. We could calculate this change in canopy conductance using Eq. (17) by integrating both sides of the equation from E_{c1} to E_{c2} for any g_{c1} to g_{c2} , but a simple algebraic derivation from the Penman-Monteith equation is easier.

The Penman-Monteith equation for a whole canopy can be written as

$$E_c = \Omega_c E_0 \quad (18)$$

where Ω_c is as we have previously defined it and

$$E_0 = \varepsilon(R_n - S)/[\lambda(\varepsilon + 1)] + g_{as}D_m/[P(\varepsilon + 1)] \quad (19)$$

Now, from Eq. (18)

$$E_{c1} - E_{c2} = (\Omega_{c1} - \Omega_{c2})E_0 \quad (20)$$

provided that E_0 is unaffected by the change in transpiration rate and surface energy balance. If the initial state is known so that Ω_{c1} and E_0 are known, then Eq. (20) can be solved for Ω_{c2} and hence g_{c2} , given the change in transpiration rate. Alternatively, we can investigate the change in Ω_c or in canopy conductance that is associated with the relative change in transpiration rate ($E_{c1}/E_0 - E_{c2}/E_0$).

The data presented by Van Bavel (1967) provide an example of changes in canopy resistance ($= 1/g_c$) that may occur in response to a diminishing availability of water in the soil. Figure 15 shows the transpiration rate, E_c , and also E_0 for a crop of alfalfa, together with calculated canopy resistances on two days during a drying spell, one near the onset of water restriction and the other a few days later when water supply had become severely limiting. From these data we see that the ratio of E_c/E_0 in the early afternoon of the second day was about half that on the first day, and that an approximately 10-fold increase in canopy resistance was necessary to achieve this reduction. More recently, Baldocchi *et al.* (1983) found that a reduction in the transpiration of a soybean crop of about one-third, as a result of water stress, was associated with a 5-fold increase in stomatal resistance.

There is a difficulty in using the data of Van Bavel because the atmospheric measurements were made at a height of only 2 m above the ground, a height at which the surface fluxes of heat and water vapour would certainly be important in setting the value of saturation deficit measured by the sensors. For example, Baldocchi *et al.* (1983) found that the saturation deficit over the soybean canopy (1.5 m above the ground)

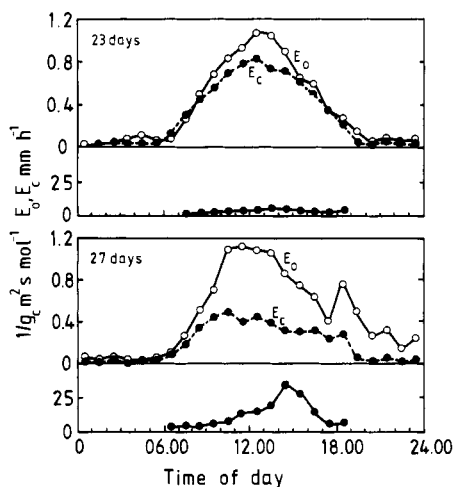


Fig. 15. Mean hourly rates of transpiration, E_c , calculated “potential” transpiration, E_o , and canopy resistance ($=1/g_c$) of alfalfa at Phoenix, Arizona, in June, 23 days (above) and 27 days (below) after the last irrigation. After Van Bavel (1967).

increased from 1.5 to 3.5 kPa at midday, as water stress reduced transpiration by about one-third. Although Van Bavel called E_o by the name “potential evaporation” (Van Bavel, 1966) and described it as the evaporation rate that would have occurred had the surface been wet, it is not really so because the reference level is too low (McNaughton and Jarvis, 1983): truly wet foliage would certainly cause a much lower saturation deficit at a height of only 2 m. Thus, the values for Ω_c , although numerically well defined from Van Bavel’s measurements, cannot be interpreted as decoupling coefficients between the crop surface and an independent atmosphere above.

An interesting comparison may be made between this experiment by Van Bavel and another well-known experiment on transpiration by water-stressed maize plants by Denmead and Shaw (1962). In the latter experiment, maize plants were grown in large pots in the field amongst a continuous canopy of unstressed plants. Water supply was restricted in the pots, so transpiration from the plants in them was ultimately reduced. However, the saturation deficit around each individual leaf of the stressed plants would have been determined solely by the weather and by the stomatal conductances of the other, unstressed plants. Thus, the experimental design prevented any feedback from the stomatal conductances of the stressed plants to the saturation deficit within the canopy. In this respect, the experiment was similar to experiments in controlled-environ-

ment chambers where feedback between transpiration and the saturation deficit around the leaves is also not usually allowed to operate. The response of transpiration to a reduction in soil water supply observed by Denmead and Shaw is, therefore, unlikely to be the same as would have been found had all of the plants in the field suffered water stress simultaneously. Had water supply to the plants been limited over the whole field, the saturation deficit within the maize canopy would have risen as the stomata closed, requiring a larger decrease in stomatal conductance to restrict transpiration. We surmise that in the latter case, stomatal conductance, and so assimilation, would have been more abruptly reduced as the drying spell progressed, along the lines of the response of E_c shown in Fig. 15. One implication of this is that there would have been a larger reduction in CO_2 flux into the leaves had the whole field been droughted than was the case for individually stressed plants. Thus, the size of an area of vegetation experiencing water stress has an important bearing on CO_2 assimilation by the stressed plants.

Similar caveats must be expressed regarding the interpretation of any treatment in a field experiment that affects the water relations of only a small proportion of the plants present. When treatments are applied to single plants or to small areas of vegetation, the feedback between transpiration and saturation deficit around the leaves will not occur to the same extent as if the treatments were applied on a larger scale. Other current examples that spring to mind include the application of antitranspirants to just a few individuals or to small areas of a crop and the manipulation of the water stress of plants in lysimeters or in small plots by the use of rainfall covers and controlled irrigation.

V. APPLICATIONS AND PROBLEMS

A. The Scale of Stomatal Control

Our consideration of the control of transpiration by stomata has covered a wide range of area scales of the transpiring unit ranging in downwind distance from 10^{-5} to 10^5 m. At appropriate points in this spectrum of scales where we can identify relevant transpiring units (stomatal pore, leaf, plant, canopy, region) we have investigated the effectiveness of stomatal control by seeking answers to the question, "What effect will a small fractional change in stomatal conductance have on the transpiration rate of the transpiring unit?" At the one extreme of transpiration through an isolated stomatal pore with dimensions of the order of 10^{-5} m, we conclude that a small change in conductance will lead to an equi-propor-

tional change in transpiration. In contrast, at the other extreme of the transpiring region up to 10^5 m across, we conclude that a small change in conductance will lead to a proportionally much smaller change in the transpiration rate, and that transpiration on this scale is largely controlled by radiation receipt and temperature. At intermediate scales the response of transpiration to a small change in conductance depends on the value of Ω taken by the transpiring unit. In general, we can say that as the area scale increases in size, Ω increases and transpiration becomes less influenced by a small change in the total conductance and more strongly dependent upon radiation. Of course, at any particular scale there may be wide variations in Ω depending on the aerodynamic roughness of the transpiring unit. For example, the value of Ω_c for an extensive area of grassland will always be larger than the value of Ω_c for an equally extensive area of forest, as shown in Table 2. But for the same kind of leaves or plants, Ω will always be much larger for those comprising an extensive canopy than it will be for isolated individuals; that is, the effectiveness of stomatal control of transpiration depends on the structural context within which a leaf or plant occurs: transpiration is more effectively changed by a change in stomatal conductance of an isolated leaf than it is by a change in the canopy conductance of a canopy of similar plants. Indeed, in the case of unstressed, aerodynamically smooth canopies of even moderate extent, changes in canopy conductance have such a small influence on transpiration that the effect can easily be overlooked.

B. The Individual versus the Crowd

If the stomata exert little control over transpiration from vegetation on a large scale, then what is the significance of the variation in stomatal conductance that occurs amongst leaves and plants making up a canopy? In our considerations of transpiration at different scales, we have been at pains to distinguish between transpiration from the unit as a whole, be it leaf, plant or canopy, and transpiration from an individual within that unit. Most vegetation is heterogenous and consists of a range of genotypes and species, sometimes of a very large number, as in tropical rain forest or chalk grassland, for example. Even within monocultures significant genetic variation amongst individuals may occur, sites within a crop are not homogenous, and weeds, of course, are often an appreciable component of the plant population. What is the significance of such small-scale variability of stomatal conductance in circumstances when the overall rate of transpiration is largely set by radiation and temperature?

The saturation deficit within a canopy depends on both the weather overhead and on the total stomatal conductance of all the leaves in the

canopy. If all the leaves change their stomatal conductance in unison, the canopy conductance will change, and so too will the saturation deficit within the canopy. The responsiveness of transpiration from the whole canopy to a change in canopy conductance depends on Ω_c , as described by Eq. (17). An individual leaf within the canopy "sees" the saturation deficit within the canopy as externally set. If a single leaf, acting alone, changes its stomatal conductance, the saturation deficit within the canopy remains almost completely unaffected. The change in transpiration rate of that leaf in response to the change in its stomatal conductance depends on Ω_l , as described by Eq. (13). The form of Eq. (13) and (17) is identical: they differ only in their respective values of Ω . Because of the additional decoupling provided by the surface layer resistance, Ω_c is always larger than the corresponding Ω_l . Thus, we may draw the general conclusion that stomata exert stronger control over transpiration from individuals acting alone than they do over the total transpiration from the crowd when all individuals act together. Furthermore, when Ω_c is large, a small change in transpiration by one or a few individuals is likely to be compensated for by an equal and opposite small change in transpiration spread over the bulk of the population. This suggests that we should often interpret movements of stomata in terms of the *relative allocation* of transpiration between leaves and plants rather than in terms of regulation of the absolute amount from the stand as a whole.

In a large-scale agricultural monoculture, for example, if the stomatal conductance of an individual plant increases, its transpiration will also increase, with the result that all the other plants downwind of it will show a minute reduction in transpiration, since they will experience an infinitesimally smaller saturation deficit. As a result of such individual control, the various leaves on a plant may have different transpiration rates and different plants may transpire at different rates, but within the externally set overall total for the canopy. In a mixture of two species such as C_3 cereal like rice and an aggressive C_4 weed like barnyard grass (*Echinochloa crus-galli*), both species experience the same saturation deficit and will transpire in relation to their own particular stomatal conductances and leaf areas within the externally set overall total. As the soil water becomes depleted, their stomatal conductances may change differentially, leading to a change in the distribution of transpiration between them (O'Toole and Tomar, 1982). Since they will both experience the same ambient CO_2 concentrations as well as the same saturation deficits, the C_4 weed is likely always to have a greater water use efficiency, and this may contribute to its competitive ability. In extensive forest too, the main source of transpiration within the canopy may redistribute from overstorey to understorey during the summer, depending on their stomatal conductances,

while the overall transpiration rate remains highly conservative (Roberts, 1983).

In an extensive short canopy made up of many different species, such as in the Canadian prairies where transpiration proceeds at close to the equilibrium rate (Mukammal and Neumann, 1977), the rate of transpiration from each species may vary widely within the externally set total. Each species experiences the same saturation deficit around the leaves, set by the external conditions and the average stomatal conductance, and each transpires at a rate set by its own stomatal conductance. An ecologist looking at one species will see evidence of stomatal control of transpiration whereas a micrometeorologist looking at the transpiration of the vegetation as a whole will see little or no evidence of stomatal control.

C. Extrapolation from Small to Large Scales

Here we draw attention to several consequences of our analysis. We have shown that the effect of a fractional change in conductance on transpiration depends on the context of the leaf appropriately represented by the scale of the transpiring unit and expressed by Ω . Clearly, problems arise in attempting to extrapolate from one scale to the next. We have drawn attention earlier, for example, to the problems encountered by Brown and Escombe (1900) and Penman and Schofield (1951) in attempting to scale up from the pore to the leaf and the leaf to the canopy, respectively. Yet plant physiologists and ecologists continue to do experiments in leaf cuvettes, plant chambers and growth rooms in the hopeful expectation that the results can be applied to unenclosed plants growing in the field (e.g., Enoch and Hurd, 1979).

The design criteria for such chambers are that the conditions of temperature and humidity around the leaves or plants should be controllable by the operator and independent of the heat and water vapour fluxes at the leaf surfaces, i.e., feedback between transpiration and the environment around the leaves is prevented. As a result, Ω_l is close to zero and a small change in stomatal conductance is very effective in bringing about a change in transpiration, as we showed in Fig. 1. We should not, however, expect that agents that show themselves to be effective in reducing stomatal conductance and transpiration in such chambers (e.g., high CO_2 , low humidity, abscisic acid, chemical and physical antitranspirants, etc.) will be equally effective in reducing transpiration from vegetation in the field where the feedbacks do operate and Ω_c is much larger. Whether or not this leads to misleading conclusions depends on the change in scale. Anti-transpirants tested in growth rooms, for example, have not, on the whole, been very successful when applied to crops in the field. High CO_2 concen-

trations very effectively reduce stomatal conductance of many C_3 and C_4 plants (e.g., Morison and Gifford, 1983), but we do not expect the current global rise in CO_2 concentrations to lead to significant reductions in transpiration at the regional scale. Since assimilation by C_4 plants is not usually limited by CO_2 concentration, we would not expect to find any increase in water-use efficiency on this scale, although such increases are readily demonstrated in pot experiments.

Problems of an opposite kind may arise with experiments in glass-houses, since these are frequently poorly ventilated, leading to poor coupling between the leaves and the air above. For example, Lake *et al.* (1969) measured much larger aerodynamic resistances over a canopy in a glasshouse than would be expected in the field. This situation can lead to the view that the stomata are even less effective in controlling transpiration from the canopy than would actually be the case in the field. Burgy and Pomeroy (1958) measured similar rates of transpiration and of evaporation of water sprayed on small plots of grass in a glasshouse, thus demonstrating complete lack of control of transpiration by the stomata. Although the plots were very small, the dry foliage was transpiring as though it were wet, a result that we would otherwise expect only on the extensive canopy or regional scales.

It follows that good design is crucial for experiments to determine the effects of a perturbation in the environment on transpiration. The effects of a change in stomatal conductance on transpiration can only be transferred from one situation to another, or one scale to another if, *inter alia*, values of Ω and of the saturation deficit around the leaves are similar at the two scales. We have already commented on the experiments of Briggs and Shantz (1916) in which potted plants were lined up on the edge of a field and the experiment of Denmead and Shaw (1962) in which potted plants were allowed to dry out within a crop otherwise well supplied with water. In neither case were these conditions met. Similar problems arise with the small field plots favoured by plant breeders. In a large field of small plots, the stomata exercise effective control of transpiration at the scale of the plot (say 3×4 m), whereas transpiration from the whole field is largely set by the weather. A particular genotype might do very well in such a small plot trial if it were to decrease stomatal conductance and conserve water through to maturity. However, when the plot of that genotype is expanded to occupy the whole field, a rather different result may be obtained because transpiration is not now significantly reduced by moderate stomatal closure.

One cannot naïvely extrapolate directly from one scale to the next. Information gained at one scale can be applied to predict what may happen at another only through the use of a model such as Eq. (12) or (15).

Such a model requires appropriate values of Ω and of the reference saturation deficit at the appropriate location as well as radiation data.

VI. CONCLUSION

To return to the conflict that we spelled out at the start, we can conclude that both the plant physiologists and ecologists working with individual leaves and plants and the meteorologists and agronomists working with extensive areas of vegetation are correct in their assessment of the control, or lack of control, of transpiration by the stomata. The conflict of opinion is not a conflict of scientific evidence but of interpretation. It is a consequence of the different scales at which the evidence has been obtained and the results interpreted. The results from either group are not applicable to the plant systems studied by the other, unless proper allowance is made for the change of scale. Awareness of the significance of scale and its consequences for interpretation, extrapolation and prediction of transpiration seems to have been largely lacking in both groups.

VII. APPENDIX A: DERIVATION OF EQUATIONS

A. For the Single Leaf

Here we develop the equations for evaporation from a single leaf, equilibrium evaporation from a single leaf, and the expression for Ω_ℓ and D_ℓ . As described in the main text, Ω_ℓ may be regarded as a decoupling coefficient between the saturation deficit at the surface of a single leaf and that in its aerial environment. It is assumed that, in the general case, the leaf is asymmetric with respect to both its stomatal conductance and the conductance of the boundary layer developed over the leaf. Our conceptual model for heat and vapour exchange from the leaf is represented in Fig. 7.

Our methods follow the usual derivation of the Penman–Monteith equation (Monteith, 1965), except that we explicitly retain separate account of exchanges from both sides of the leaf. For convenience the subscript ℓ , for leaf, is omitted from E_ℓ in the following treatment. Thus, we write the equation for latent heat transfer from the leaf as

$$\lambda E = \lambda E_1 + \lambda E_2 = \frac{c_p}{\gamma} \left[\frac{e^*(T_\ell) - e_a}{1/g_{s1} + 1/g_{bv1}} \right] + \frac{c_p}{\gamma} \left[\frac{e^*(T_\ell) - e_a}{1/g_2 + 1/g_{bv2}} \right]$$

or

$$\lambda E = (c_p/\gamma)[e^*(T_\ell) - e_a]G_v = (\lambda/P)[e^*(T_\ell) - e_a]G_v \quad (A1)$$

where G_V is the total conductance for water vapour from both sides of the leaf, and is given by

$$G_V = 1/(1/g_{s1} + 1/g_{bv1}) + 1/(1/g_{s2} + 1/g_{bv2}) \quad (A2)$$

Both fluxes and conductances are expressed on a consistent leaf *surface* area basis in units of $\text{mol m}^{-2} \text{sec}^{-1}$. Thus, λ is the molar latent heat of vaporisation of water and c_p is the molar heat capacity of dry air: in consistent units, $c_p/\gamma = \lambda/P$, where γ is the psychrometric constant. The symbols for all of the quantities are defined in Appendix B.

Similarly, sensible heat transfer from both sides of the leaf is

$$\begin{aligned} H &= H_1 + H_2 = c_p(T_\ell - T_a)g_{bH1} + c_p(T_\ell - T_a)g_{bH2} \\ &= c_p(T_\ell - T_a)G_H \end{aligned} \quad (A3)$$

where G_H is the total conductance for sensible heat and is given by

$$G_H = g_{bH1} + g_{bH2} \quad (A4)$$

Now Eq. (A1) can be expanded into the form

$$\lambda E = (c_p/\gamma)[e^*(T_\ell) - e^*(T_a) + e^*(T_a) - e_a]G_V$$

and so written as

$$\lambda E = (c_p/\gamma)[s(T_\ell - T_a) + D_a]G_V \quad (A5)$$

where s is the slope of the saturation vapour pressure versus temperature relationship at the leaf surface, i.e.,

$$s = [de^*(T)/dT]_{T=T_\ell}$$

and D_a is defined by

$$D_a = e^*(T_\ell) - s(T_\ell - T_a) - e_a$$

Thus, D_a is a linear approximation to the true saturation deficit, and differs from it minimally over the small temperature difference $(T_\ell - T_a)$. In defining s as the value at the leaf surface rather than the mean value at $(T_\ell + T_a)/2$, and using the linearised form for D_a , we differ slightly from usual practice, but make these adjustments to keep the argument more consistent with our later treatment of the larger scale.

Equation (A5) is inconvenient because T_ℓ is a variable whose value is unknown. An equation for $(T_\ell - T_a)$ can be developed from Eq. (A3) using also the energy balance relationship

$$H + \lambda E = R_n \quad (A6)$$

so that

$$T_\ell - T_a = (R_n - \lambda E)/(c_p G_H) \quad (A7)$$

Substitution of this into Eq. (A5) eliminates $(T_\ell - T_a)$ to give

$$\lambda E = (c_p/\gamma)[s(R_n - \lambda E)/(c_p G_H) + D_a]G_V$$

or, upon rearrangement,

$$\lambda E = \frac{\varepsilon R_n + c_p D_a G_H/\gamma}{\varepsilon + G_H/G_V} \quad (\text{A8})$$

where $\varepsilon = s/\gamma = (de^*/dT)\lambda/(c_p P)$ is a strong function of temperature.

In this equation we shall assume that R_n has a fixed value. This is not strictly true, since R_n depends on the variable leaf temperature and so is not completely known at the outset. Allowance for this could have been included in our analysis using the device of a radiative conductance (Monteith, 1973), but the ensuing algebraic difficulties tend to obscure the most important features of the changes in transpiration from leaves resulting from changes in stomatal conductance.

Although Eq. (A8) is apparently simple in form, a great deal of algebraic complexity is concealed within G_H and, particularly, G_V . To avoid the difficulties of the general case, here we treat only two particular cases; the symmetrical amphistomatous leaf where $g_{b1} = g_{b2} = g_b$ and $g_{s1} = g_{s2} = g_s$, and the hypostomatous leaf where $g_{s2} = 0$. For simplicity, we also assume that the ratio $g_{bH}/g_{bV} = 1$, rather than the more probable value of 0.93.

For the symmetrical amphistomatous leaf, the ratio of total conductances to heat and to water vapour G_H/G_V reduces to $(1 + g_b/g_s)$ and Eq. (A8) becomes

$$\lambda E = \frac{\varepsilon R_n + 2c_p D_a g_b/\gamma}{\varepsilon + 1 + g_b/g_s} \quad (\text{A9})$$

This is very familiar (e.g., Monteith, 1965), except that the factor 2 arises in the second term of the numerator as a result of our use of conductances defined on a single surface area basis.

If the leaf boundary-layer conductances become very small, then Eq. (A9) approaches the limit

$$\lambda E_{\text{eq}} = \varepsilon R_n/(\varepsilon + 1) \quad (\text{A10})$$

This is the evaporation rate that would obtain from a symmetrical amphistomatous leaf if it were to become decoupled from the air around by very thick boundary layers. The evaporation rate in Eq. (A10) is often known as the "equilibrium evaporation rate" (e.g., Slatyer and McIlroy, 1961; McNaughton and Jarvis, 1983), but, as shown below, other "equilibrium" values of λE can obtain if the heat and water vapour pathways are differ-

ent. When g_b is small, the saturation deficit at the surface of the leaf, D_ℓ , must adjust, since

$$\lambda E = (c_p/\gamma)(g_{s1}D_{\ell 1} + g_{s2}D_{\ell 2}) = (c_p/\gamma)2g_s D_\ell \quad (\text{A11})$$

must still apply. Thus, the saturation deficit at the surface of the leaf approaches an equilibrium value that can be found by equating λE in Eq. (A11) to that in (A10), giving

$$D_{\text{eq}} = \gamma \varepsilon R_n / (\varepsilon + 1) c_p 2g_s \quad (\text{A12})$$

If, on the other hand, the boundary-layer conductance is very large, then Eq. (A9) approaches the limit

$$\lambda E_{\text{imp}} = (c_p/\gamma)2g_s D_a \quad (\text{A13})$$

Equation (A13) is similar to Eq. (A11) except that the boundary-layer conductances are now so small that the ambient saturation deficit is "imposed" at the leaf surface with the result that D_ℓ becomes D_a .

A leaf operates between these two limits, and we can write Eq. (A9) as

$$E = \Omega_\ell E_{\text{eq}} + (1 - \Omega_\ell) E_{\text{imp}} \quad (\text{A14})$$

and

$$D_\ell = \Omega_\ell D_{\text{eq}} + (1 - \Omega_\ell) D_a \quad (\text{A15})$$

where

$$\Omega_\ell = (\varepsilon + 1) / (\varepsilon + 1 + g_b/g_s) \quad (\text{A16})$$

The Ω_ℓ can be regarded as a measure of the decoupling between conditions at the leaf surface and those in the free airstream. It takes values in the range 0 to 1. When $\Omega_\ell \rightarrow 0$, conditions at the leaf surface are very strongly coupled to those in the surrounding air and $D_\ell \rightarrow D_a$. When $\Omega_\ell \rightarrow 1$, conditions at the leaf surface are very poorly coupled to those of the free airstream and D_ℓ finds its own value by local equilibration.

Only a minority of leaves are symmetrical with respect to stomatal conductance (Ticha, 1982). Perhaps even fewer are symmetrical with respect to boundary-layer conductance, since most leaves are curved or creased rather than flat. For a hypostomatous leaf when $g_{s2} = 0$, the ratio G_H/G_V reduces to $[(g_{b1} + g_{b2})/g_{s1} + g_{b2}/g_{b1} + 1]$, and this simplifies further to $2(g_b/g_{s1} + 1)$ if $g_{b2} = g_{b1}$. This latter result is implicit in the treatment by Cowan and Troughton (1971) and is given by Thorpe (1978). However, the general case of unequal boundary-layer conductances does not appear to have been considered previously.

For the general hypostomatous leaf with stomata only on side 1, Eq. (A8) leads to

$$\lambda E = \frac{\varepsilon R_n + c_p D_a (g_{b1} + g_{b2})/\gamma}{\varepsilon + 1 + (g_{b1} + g_{b2})/g_{s1} + g_{b2}/g_{b1}} \quad (\text{A17})$$

This equation is interesting because it suggests that active leaf rolling or folding to produce differences in the ratio g_{b2}/g_{b1} might control transpiration as effectively as changes in stomatal conductance. Some plants, such as rice (O'Toole and Cruz, 1980) and fescue (*Festuca arundinacea*) (Renard and Demesse-macker, 1983), seem to be particularly well adapted to exploit this form of control.

If we pursue the same arguments as before and let g_{b1} and g_{b2} tend to zero, whilst maintaining a constant ratio g_{b2}/g_{b1} , then we find

$$\lambda E_{eq} = \varepsilon R_n / (\varepsilon + 1 + g_{b2}/g_{b1}) \quad (\text{A18})$$

The imposed evaporation rate reduces to half of that for the amphistomatous leaf, since stomata are now on only one side of the leaf, so

$$\lambda E_{imp} = (c_p/\gamma) g_{s1} D_a \quad (\text{A19})$$

The Ω_ℓ equations (A14) and (A15) still apply, but with

$$D_{eq} = \gamma \varepsilon R_n / (\varepsilon + 1 + g_{b2}/g_{b1}) c_p g_{s1} \quad (\text{A20})$$

at the transpiring surface of the leaf, and

$$\Omega_\ell = \frac{\varepsilon + 1 + g_{b2}/g_{b1}}{\varepsilon + 1 + (g_{b1} + g_{b2})/g_{s1} + g_{b2}/g_{b1}} \quad (\text{A21})$$

In the case of either the symmetrical amphistomatous leaf or the hypostomatous leaf, we can derive a relationship for the response of E to a small change in g_s from Eq. (A14) and write

$$\frac{dE}{E} = E_{eq} \frac{\delta \Omega_\ell}{\delta g_s} - E_{imp} \frac{\delta \Omega_\ell}{\delta g_s} - \Omega_\ell \frac{\delta E_{imp}}{\delta g_s}$$

By substituting the appropriate values of E_{eq} , E_{imp} and Ω_ℓ for the two cases, we obtain an equation of similar form for either case, which can be written as

$$dE/E = (1 - \Omega_\ell) dg_s/g_s \quad (\text{A22})$$

where Ω_ℓ is defined by Eq. (A16) for the symmetrical amphistomatous leaf and by Eq. (A21) for the hypostomatous leaf. Although the same suite of equations, (A14), (A15) and (A22), describe transpiration in these two quite different cases, similar forms do not appear to be available for the general case of the asymmetrical leaf, since in the general case equilibration proceeds differently on the two transpiring leaf surfaces, giving two

different values of D_{eq} . In the two cases we have treated, either D_{eq} on both sides is the same or only one side need be considered.

B. For the Canopy

Equations for a canopy follow directly from the treatment of a single leaf, since in the "big leaf" canopy model approximation a canopy is analogous to a single leaf with convective heat and water vapour transport from one side only. For this case G_H in Eq. (A8) becomes the surface-layer aerodynamic conductance for heat, g_{as} , and G_V reduces to $(1 + g_{as}/g_c)$ where g_c is now the "canopy conductance." Also, a heat flux term to describe conduction of heat into storage must be included in the energy-balance Eq. (A6), so the right-hand side becomes $(R_n - S)$, where S is the heat flux density into the canopy airmass and biomass and into the soil. Finally, a modification must be made to our definition of saturation deficit, since we now deal with changes over significant vertical heights and corrections to allow for pressure changes are needed. Thus, we replace temperature, T , with the potential temperature, Θ , in all of the equations and reduce e in the ratio of the surface pressure, P_o , to P_z , so that the general definition of D becomes

$$D_z = e^*(\Theta_o) - s(\Theta_o - \Theta_z) - e_a P_o / P_z \quad (A23)$$

We have chosen the reference height for Θ_o to be at the canopy surface, rather than follow the usual meteorological practice of sea level, so that $\Theta_o \equiv T_o$. D_m is then the potential saturation deficit and is the saturation deficit that a parcel of air would have if brought down adiabatically from some height to the surface.

With these changes we can adapt the leaf equation, (A8), to a canopy equation and write

$$\lambda E_c = \frac{\varepsilon(R_n - S) + c_p D_m g_{as} / \gamma}{\varepsilon + 1 + g_{as} / g_c} \quad (A24)$$

and so

$$\lambda E_{eq,c} = \varepsilon(R_n - S) / (\varepsilon + 1), \quad (A25)$$

$$\lambda E_{imp,c} = (c_p / \gamma) g_c D_m \quad (A26)$$

and

$$\Omega_c = (\varepsilon + 1) / (\varepsilon + 1 + g_{as} / g_c) \quad (A27)$$

Equations of similar form to (A14) and (A15) can now be written for the canopy in terms of Ω_c with D_{eq} given by

$$D_{eq} = \gamma \epsilon (R_n - S) / (\epsilon + 1) c_p g_c \quad (A28)$$

The following equation, corresponding to Eq. (A22), is obtained for a small change in transpiration rate from the canopy:

$$dE_c/E_c = (1 - \Omega_c) dg_c/g_c \quad (A29)$$

VIII. APPENDIX B: LIST OF SYMBOLS AND ABBREVIATIONS

a	average cross-sectional area of a stomatal pore (m^2)
c_p	molar heat capacity of dry air at constant pressure ($\text{J mol}^{-1} \text{K}^{-1}$)
D	water vapour saturation deficit of air (for subscripts, see below) (kPa)
D_{eq}	equilibrium saturation deficit [defined by Eqs. (A12) and (A20)] (kPa)
\mathcal{D}_w	molecular diffusivity of water vapour in air ($\text{m}^2 \text{sec}^{-1}$)
d	major dimension of a leaf (mm)
E	total transpiration rate (subscripts ℓ and c for leaf and canopy, respectively) ($\text{mol m}^{-2} \text{sec}^{-1}$)
E_{eq}	equilibrium transpiration rate [defined by Eqs. (A10), (A18) and (A25)] ($\text{mol m}^{-2} \text{sec}^{-1}$)
E_{imp}	imposed transpiration rate [defined by Eqs. (A13), (A19) and (A26)] ($\text{mol m}^{-2} \text{sec}^{-1}$)
E_0	transpiration without stomatal limitation [defined by Eq. (19)] ($\text{mol m}^{-2} \text{sec}^{-1}$)
E_p	transpiration rate through a stomatal pore (mol sec^{-1} per pore)
e	partial pressure of water vapour in air (for subscripts, see below) (kPa)
e^*	saturation vapour pressure of water vapour in air (kPa)
G	total transfer conductance (subscripts H and V for sensible heat and water vapour, respectively) ($\text{mol m}^{-2} \text{sec}^{-1}$)
g	surface conductance (for subscripts, see below) ($\text{mol m}^{-2} \text{sec}^{-1}$)
g_p	conductance of a stomatal pore (mol sec^{-1} per pore)
H	sensible heat flux density ($\text{J m}^{-2} \text{sec}^{-1}$)
h	height of canopy (m)
l	effective length of diffusion pathway through a stomatal pore (m)
n	number of stomatal pores per unit area of leaf surface (mm^{-2})

P	atmospheric pressure (kPa)
PBL	planetary boundary layer
R	Universal Gas Constant (8.3144) ($\text{J mol}^{-1} \text{K}^{-1}$)
R_n	net radiation flux density ($\text{J m}^{-2} \text{sec}^{-1}$)
S	flux density of heat into storage in canopy and soil ($\text{J m}^{-2} \text{sec}^{-1}$)
s	slope of the relation between saturation vapour pressure and temperature [$de^*(T)/dT$] (kPa K^{-1})
T	air temperature (for subscripts, see below) ($^{\circ}\text{C}$)
t	time (day)
u	wind speed (m sec^{-1})
\bar{V}_w	partial molar volume of water ($\approx 18 \times 10^{-6}$) ($\text{m}^3 \text{mol}^{-1}$)
α	Priestley–Taylor coefficient (E/E_{eq})
γ	psychrometric constant ($c_p P/\lambda$) (kPa K^{-1})
ε	$s/\gamma = s\lambda/(c_p P)$
Θ	potential temperature (for subscripts, see below) (K)
λ	molar latent heat of vaporisation of water (J mol^{-1})
ψ	water potential (MPa)
Ω	decoupling coefficient [defined by Eqs. (A16), (A21) and (A27)] (subscripts ℓ and c for leaf and canopy, respectively)

Other Subscripts

ℓ, a	indicate at the leaf surface and in the free airstream outside the leaf boundary layer, respectively
$o, m, z,$	indicate at the effective canopy surface, in the mixed layer and at any height, z , above the surface of the ground, respectively
s, c	indicate stomatal conductance of one leaf surface and surface conductance of the canopy, respectively
b, as	indicate the boundary layers of one leaf surface and of the canopy, respectively
$1, 2$	indicate either the abaxial and adaxial surfaces of a leaf [Eqs. (A11–A21)] or first and second occasions [Eq. (20)], respectively

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