Tansley Review No. 59. Leaf Boundary Layers

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Tansley Review No. 59
Leaf boundary layers

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SUMMARY

Studies of heat and mass exchange between leaves and their local environment are central to our understanding of plant-atmosphere interactions. The transfer across aerodynamic leaf boundary layers is generally described by non-dimensional expressions which reflect largely empirical adaptations of engineering models derived for flat plates. This paper reviews studies on leaves, and leaf models with varying degrees of abstraction, in free and forced convection. It discusses implications of findings for leaf morphology as it affects – and is affected by – the local microclimate. Predictions of transfer from many leaves in plant communities are complicated by physical and physiological feedback mechanisms between leaves and their environment. Some common approaches, and the current challenge of integrating leaf-atmosphere interactions into models of global relevance, are also briefly addressed.

Key words: Leaf boundary layer, aerodynamic resistance and conductance, diffusion, transpiration, plant-atmosphere interaction, morphological adaptation.

I. INTRODUCTION

Physical life, as we know it, depends on exchange processes between vegetation and the atmosphere, which are usually described through an energy balance or in terms of transfer of water vapour, CO_2, trace gases and particle pollutants. The study of plant communities, like that of any other community, must be based on insight into the behaviour of their constituent elements, although mutual interaction and feedback mechanisms make the community more than the sun of its parts. In the case of vegetation, attention to the leaf – and its aerodynamic boundary layer – must be an integral part of any effort to understand how solar radiation drives those exchange processes without which life on this planet would be impossible.

The enormous variety in shape and size of leaves has long been an object of fascination and speculation. Differences occur within species, for example as sun-shade dimorphism, very likely as part of an adaptive response to different habitats. The advent of genetic engineering has raised the question of man-made manipulation of leaf shape, changing the micro-environment of the leaf for optimum crop performance in terms of photosynthesis or water use, or for reduction of on-leaf development of plant pathogens.

This review deals with the air layer adjacent to the leaf surface, the so-called leaf boundary layer (BL) (see Appendix for symbols and abbreviations). The concept of the BL was introduced by Prandtl (1904) (as cited by Schlicting, 1968, pp. 24–25). It denotes a zone where wind speed is non-negligibly reduced by surface friction. The airflow within the BL may be laminar or turbulent, but even if the latter is the case there will be some distance close to the surface where turbulence is suppressed and transfer of heat and mass effected predominantly by molecular diffusion. This imposes a physical restriction on transfer, the so-called 'boundary layer resistance'. The thickness δ of the laminar leaf BL at a distance x downwind from the leading (upwind) edge of the leaf, can be estimated from the kinematic viscosity of air ($\nu = 1{\cdot}5 \times 10^{-5}\ m^2 s^{-1}$), and the wind speed u through the semi-empirical expression $\delta \approx \sqrt{(\nu x/u)}$ (see e.g. the summary given in Nobel, 1991, pp. 363–366, or the more rigorous treatment in Schlichting, 1968, pp. 130–131). This means that BL thickness 5 cm from the upwind edge would be expected to vary between 2·8 mm and 0·28 mm, for winds speeds between 0·1 and 10 m^{-1}. On large leaves, in low wind conditions, the BL thickness may exceed 1 cm. It should be noted that the definition of BL thickness in terms of departure from free stream velocity is arbitrary, since velocity profiles approach free stream values asymptotically. The expression given above corresponds approximately to the 'displacement thickness' of streamlines over rigid flat plates as defined in fluid dynamics (e.g. Schlichting, 1968, pp. 130–131), but reduced by factor of $\approx 1{\cdot}7$ due to the irregular shape and motion of leaves. BL thickness, defined as the distance where velocity attains 99% of free steam velocity, would be approximately three times larger (Schlichting, 1968, pp. 130–130). Figure 1*a* shows measurements of velocity profiles in the BL of a *Populus* leaf by Grace & Wilson (1976). In spite of irregularities introduced by leaf curvature, the growth of BL thickness with increasing downwind distance is evident.

For well ventilated canopies, the BL itself represents a minor obstruction (of $\approx 20\%$) to diffusion processes between the leaf and its environment, but it may exercise an important controlling function on stomatal exchange, as will be discussed later. Its role increases in conditions of low wind speed, such as in greenhouse cultivation and in the local environment of plants growing close to the ground. For large leaves like *Tectona grandis* L.f. or *Gmenlina arborea* L., which are characterized by high stomatal conductance and high BL resistance, it may become the dominant factor in diffusion pathways (Grace, Fasehun & Dixon, 1980).

Like all diffusion processes, the transfer of heat or

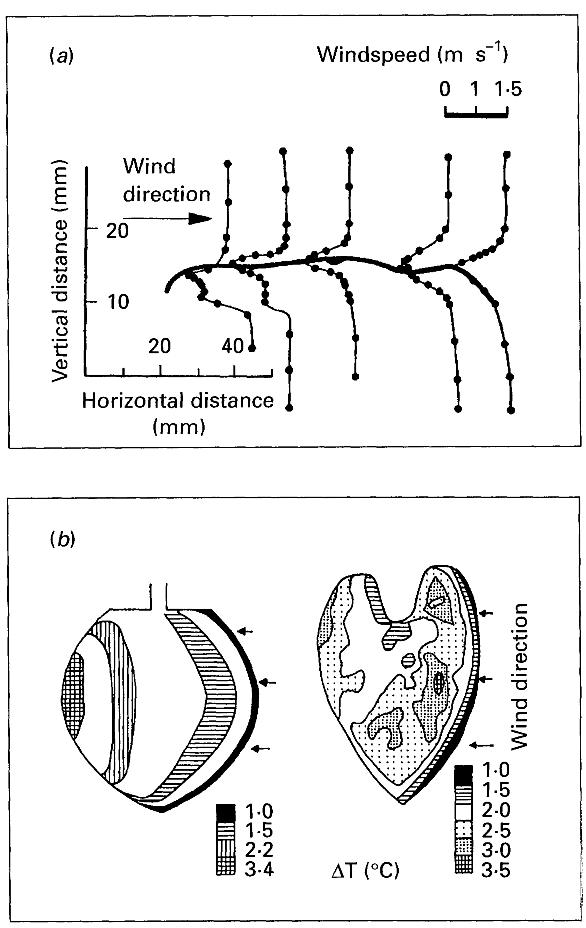

Figure 1. (*a*) Profiles of mean wind adjacent to a *Populus* leaf (from Grace & Wilson, 1976); (*b*) Temperature differences observed between surface of artificial and natural leaf, and ambient air (from Wigley & Clark, 1974).

gases between a leaf and its air envelope may be described by Fick's Law of Diffusion, as a product of the concentration gradient of the diffusing quantity and a 'diffusivity' which characterizes the physical mechanism of transport. Having units of [length^2 time^{-1}], it can be interpreted as the product of exchange length and exchange velocity. For molecular diffusion, the exchange length is determined by the mean free path of molecules, and the exchange velocity by their mean kinetic energy. For gases at normal environmental temperatures (300 °K), mean free path and exchange velocity are of the order of $\approx$ 45 nm and 500 m s^{-1}, respectively, giving molecular diffusivities of the order of $2 \cdot 3 \times 10^{-5}$ m^2 s^{-1}. By contrast, exchange lengths in vegetation are comparable to the spacing between leaves or plants, and turbulent exchange velocities of the order of cm s^{-1} or m s^{-1}, so that turbulent diffusivities are several orders of magnitude larger than molecular ones. According to Fick's Law, and for a given flux density of heat or mass, the small molecular diffusivities near the leaf surface are associated with high gradients. These pronounced gradients of wind speed, temperature and moisture near the leaf surface not only serve to insulate the leaf against ambient environmental conditions, but assure a microclimate for insects or microorganisms that may diverge considerably from ambient canopy conditions. The leaf BL should be seen, therefore, not only as a controlling agent on exchange processes of fundamental importance to the energy balance, to transpiration and to photosynthesis, but also as a potentially interesting micro-environment.

This review will describe the effect of the magnitude of leaf BL on heat and mass transfer processes through a number of studies on natural leaves, physical and numerical leaf models under more or less controlled conditions, and engineering studies in so far as they address questions of relevance to leaf transfer. Leaves are highly differentiated physical and biological entities. No two leaves are exactly alike and, as a consequence, results of observations on natural leaves are not easily generalized. For this reason, studies in more or less 'abstract' systems, under controlled conditions, have found broad acceptance. We will see a variety of observations, with divergence of results attributable to variations in technique and sophistication, more often – perhaps – to subtle differences in experimental conditions that may not always have been recognized or documented. We will briefly review effects of leaf morphology on transfer processes and, finally, the challenge of integrating the effect of leaf BL thicknesses into plant exchange processes at scales relevant to regional and global models for the balance of energy, water, CO_2 or trace gases.

This review will focus primarily on studies of heat and moisture transfer, which constitute the bulk of experimental leaf BL investigations. However, arguments apply equally well to the exchange of CO_2, with appropriate adjustment for the difference in molecular properties where indicated. The transfer of momentum (i.e. the physical force exerted on the leaf by the flow) will be considered only implicitly, in so far as it affects leaf motion and BL structure.

II. EARLY STUDIES

In their pioneering analyses of leaf energy transfer in free and forced convection (i.e. in still and moving air), Brown & Escombe (1905) and Brown & Wilson (1905) defined a 'thermal diffusivity' as a measure of energy loss per unit area and per unit temperature excess between leaf surface and ambient air. From the few available engineering-type heat transfer studies they knew that heat transfer 'varies greatly with size and shape of the cooling body'. Their experiments on leaf sections suggested the not unreasonable heat loss rates (in current SI units) of 8·4 to 25·2 W m^{-2} deg(C or K)$^{-1}$, as air velocity (u) in their wind tunnel increased from 0 to 2·3 m s^{-1}, with a suggested linear increase for small u. The $u^{0 \cdot 5}$ velocity dependence for laminar flow over flat surfaces was established later (e.g. Fage & Faulkner, 1933). The first attempts to determine empirical relationships between evaporation and dimensions of various leaf models appear to date back to Walter (1926). The 'thermal emissivity' defined above roughly corresponds to Huber's (1935) 'Waermeaustausch' (heat exchange) coefficient but, in contrast to our current definition, it included energy loss by radiation as well as convection. The energy balance studies by Brown and coworkers suggested that leaf transfer in forced and free convection typically differed in magnitude by factors of about 10, in contrast to earlier speculations which had run as high as factors of 100 to 10000 (!).

Raschke (1956 and 1960) formulated the first physically based leaf model incorporating BL concepts. While stationed in India, he had started to make observations about the relationship between leaf size and climate zone or position in the canopy. Specific questions, pertinent at the time (1950s), concerned the link between leaf size and transpiration: are smaller leaves favoured in water conservation because cooling is more effective, lowering surface temperature and vapour pressure, or at a disadvantage because of the increased transfer efficiency conferred by a thinner BL? Answers were considered to be 'practically impossible' (Curtiss & Clark, 1950) because of the variability in radiation, air temperature and wind. Raschke addressed such questions on the basis of a physical 'leaf' with reactionless (but adjustable) stomatal exchange. He considered the leaf BL thickness to increase according to $\sqrt{x}$ along the downwind distance x (as discussed in section I), so that each point on the leaf had its own (local) heat transfer effectiveness. Local and average heat transfer were determined to be inversely proportional to BL thickness and proportional to $u^{0.5}$ in laminar flow, in agreement with contemporary classical heat transfer literature. Some empirical relationships between leaf dimension (shape) and transfer (Walter, 1926) were incorporated into a shape-dependent constant c, and heat transfer expressed by $c\, L^{-0.3}u^{0.5}$, where L is the leaf dimension in the direction of flow. Raschke's semi-empirical results are in general, quantitative agreement with later similar studies.

In contrast to earlier studies which tried to link transpiration to evaporation from an evaporimeter through a 'transpiration factor', Raschke expressed transpiration as a function of BL thickness and vapour pressure difference between leaf and ambient air, with a proportionality constant originally defined as a 'Wasserbenetzungsfaktor' (moistening factor). The latter was subsequently replaced by the stomatal and cuticular diffusion resistance (Raschke, 1960), in an analogy with electrical resistances previously suggested by Williams & Amer (1957).

Raschke (1956) calculated, through an energy balance, the temperature difference between leaf and air for different leaf sizes and climate types. While these estimates suffered from lack of stomatal feedback control, they illustrated the great potential influence of leaf dimension on transfer. In general, the Raschke (1956, 1960) papers may stand as a summary of the insights of their day, stressing points of broad validity such as the fact that 'a plant is practically never in thermodynamic equilibrium with its environment', the possibility of plant morphology as an adaptive evolutionary strategy, the conclusion that calculations and observations 'do not suffice as a proof that the relations and values obtained by using physical models are representative' and that 'a theoretical approach to non-stationary processes will be... difficult'.

III. THE FORMAL DESCRIPTION OF LEAF TRANSFER

1. *Dimensionless description of transfer*

(*a*) *BL conductance and resistance*. The transfer of heat or mass may be expressed through Fick's law, as mentioned in Section I. A very common alternative, used e.g. by Raschke (1956 and 1960) as discussed above, is based on the integrated form of Fick's law, written as the product of a conductance term (transfer coefficient h) and the differences ($\triangle$) of temperature or concentration c between the leaf surface and a point outside the BL. The flux densities for heat F_H (in units of W m^{-2}) and mass F_m (in units of kg m^{-2} s^{-1}) may then be written as

$$F_H = h_H \Delta T = \rho c_p h_T \Delta T \quad \text{and} \quad F_M = h_M \Delta c. \qquad (1)$$

With ρc_p the volumetric heat capacity of air, the units of the conductances h_H, h_T and h_M in (1) are W m^{-2} K^{-1}, m s^{-1} and m s^{-1}, respectively. The dimensional equality between h_T and h_M implies that the numerical values for these two parameters will be similar to the extent that the transport mechanisms for heat and mass across the BL are similar. For moisture transfer (transpiration), the vapour flux F_V (in units of kg m^{-2} s^{-1}), or latent heat flux λE (in units of W m^{-2}), may also be expressed in terms of the difference in vapour pressure e across the BL as

$$F_v = h_M \frac{\rho c_p}{\gamma \lambda} \Delta e \quad \text{and} \quad \lambda E = \lambda F_v = h_M \frac{\rho c_p}{\gamma} \Delta e. \qquad (2)$$

The 'psychrometric constant' γ (≈ 66 Pa °K^{-1}) is defined as $c_p P/(\lambda \epsilon)$, with c_p the specific heat at constant pressure P of air, λ the latent heat of vapourization of water, and ϵ the ratio of molecular mass of water to air ($\approx 0{\cdot}62$).

The aerodynamic resistance to transfer r_a is defined as the inverse of the conductance h. Typically, aerodynamic resistances vary from < 1 cm s^{-1} to several cm s^{-1}, considerably lower than stomatal resistances except in low wind conditions or for very large leaves. The further review given below will use either resistance or conductance concepts, as suggested by the context.

The surface concentration of water vapour or CO_2 will depend on the state of stomatal opening. This may be expressed in (1) by replacing the surface concentration by the concentration in the sub-stomatal cavity, and by expressing the resistance as a sum of stomatal resistance (r_s) and aerodynamic resistance (r_a) acting in series, assuming that conductance across the leaf epidermis is negligible. In analogy with electrical networks, the heat transfer coefficient h_T from upper (U) and lower (L) sides of a leaf can be written as the inverse of the associated two resistances acting in parallel, as $h_T = [(1/r_a^U)+(1/r_a^L)]$. Similarly, moisture transfer from both sides, with stomatal and BL resistance acting in series on each side, would be defined by $h_M = [(1/(r_a^U+r_s^U)+1/(r_a^L+r_s^L)]$.

(*b*) *Similarity numbers*. For convenience of scaling and intercomparison of results obtained in different physical systems, conductances for heat and mass in forced and free convection are usually written in the dimensionless form of Nusselt (Nu) and Sherwood (Sh) numbers, respectively. They are specified as functions of the molecular diffusion properties of the fluid, Prandtl (Pr) and Schmidt (Sc) numbers, respectively, as well as of a parameter characterizing the nature of the flow. In forced convection, the Reynolds number (Re) expresses the dynamics of the flow as the ratio of inertial to friction forces, and in free (or 'natural') convection the Grashof number (Gr) may be interpreted as the product of buoyancy force (induced by surface heating) and inertial force, divided by the square of friction forces. Nu, Sh, Pr, Sc, Re and Gr are defined as follows:

dimensionless heat transfer coefficient

$$\mathrm{Nu} = \frac{h_T L}{\alpha} = \frac{h_H L}{k} \tag{3}$$

dimensionless mass transfer coefficient

$$\mathrm{Sh} = \frac{h_M L}{D} \tag{4}$$

$$\mathrm{Pr} = \frac{\nu}{\alpha} \quad \mathrm{Sc} = \frac{\nu}{D} \quad \mathrm{Re} = \frac{uL}{\nu} \quad \mathrm{Gr} = \frac{\beta g L^3 \Delta T}{\nu^2}. \tag{5}$$

Parameters (in addition to those already defined in this section) are: 'characteristic dimension' of the object L (section III.4); thermal diffusivity of air α; thermal conductivity of air k; molecular diffusivity of mass (CO_2 or H_2O) in air D; kinematic viscosity of air ν (see section I); mean wind speed u; coefficient of thermal volumetric expansion $\beta = ((1/V)dV/dT) \approx T(°K)^{-1})$, and gravitational acceleration g. The values of Pr and Sc (for H_2O and CO_2) in air, averaged for temperatures between -5 °C and 45 °C, are 0·705 and 0·63, respectively (e.g. Monteith & Unsworth, 1990; Appendix A2). Values of Re for leaves with characteristic dimensions of 2 cm (or 20 cm) would be 1333 (or $1{\cdot}33 \times 10^4$) for every m s^{-1} in wind speed. In still air, Gr for leaves of the same dimension would be 1163 (or $1{\cdot}16 \times 10^6$) for every degree (°C or °K) in temperature difference between the leaf and its environment.

2. *Description of transfer in forced convection*

(*a*) *The Pohlhausen equation.* Pohlhausen (see e.g. Schlichting, 1968, pp. 278–289) derived an equation for the heat exchange between a point x downwind from the leading edge of a flat plate of uniform temperature in steady-state, laminar air flow as

$$h_{T,x} = \frac{0{\cdot}332}{\mathrm{Pr}^{0{\cdot}66}}\left(\frac{u\nu}{x}\right)^{1/2}$$

so that

$$\mathrm{Nu}_x = 0{\cdot}332\ \mathrm{Pr}^{0{\cdot}33}\ \mathrm{Re}_x^{\ 0{\cdot}5}, \tag{6}$$

where Nu_x is the local dimensionless heat transfer coefficient and Re_x the Reynolds number based on x as the characteristic length. When integrated over a rectangular plate of length L, we obtain an average plate transfer coefficient h_T of

$$h_T = \frac{\int^L h_{T,x}\, dx}{L} = \frac{0{\cdot}664\ \mathrm{Pr}^{-0{\cdot}66}\ \mathrm{Re}^{0{\cdot}5}\nu}{L}$$

so that

$$\mathrm{Nu} = \frac{h_T L}{\alpha} = 0{\cdot}664\ \mathrm{Pr}^{0{\cdot}33}\ \mathrm{Re}^{0{\cdot}5}. \tag{7}$$

Similarly, for mass transfer, the Polhlhausen equation can be written as $\mathrm{Sh} = 0{\cdot}664\ \mathrm{Sc}^{1/3}\ \mathrm{Re}^{1/2}$. The general validity of the Pohlhausen equation, with appropriate modifications for leaf transfer, will be documented below. It should be stressed that this BL description is two-dimensional (based e.g. on streamwise and vertical orientation on a horizontal plate) and ignores effects of finite plate width in the cross-stream direction ('edge effects').

On the basis of (7), and considering the definitions of Nu and Sh in (3) and (4), the ratio of BL resistances to the transfer of heat and mass is $r_H/r_M = h_M/h_T = (\mathrm{Sh}\,D)/\mathrm{Nu}\,\alpha) = (D/\alpha)^{2/3}$ or $\mathrm{Le}^{-2/3}$, where the Lewis number Le is defined as the ratio of Schmidt and Prandtl numbers. Substituting the appropriate molecular diffusivities of heat, water vapour and CO_2 in air, these ratios are of the order of 0·93 for r_{heat} *vs.* $r_{\text{water vapour}}$ and 1·32 for r_{heat} *vs.* r_{CO2} in fully convective flow.

(*b*) *Uniform temperature vs. uniform flux.* Thin plant leaves, with a thermal conductivity even below that of water (i.e. $k < 0{\cdot}6$ W m^{-1} °K^{-1}) (Vogel, 1984), tend to establish an approximate local energy balance at any point on the surface, where available net radiation balances the exchange of sensible and latent heat. Assuming radiation is uniform across the leaf, and transpiration small relative to radiation, the local surface temperature will adjust in such a way that heat transfer across the (variable) BL will approximately balance radiation terms. This leads to a situation of variable surface temperature (Fig. 1*b*) but uniform heat flux. In this case, the local Nu number (Nu_x) is given by $0{\cdot}453\ \mathrm{Pr}^{0{\cdot}33}\ \mathrm{Re}_x^{\ 0{\cdot}5}$ which, when integrated over a rectangular 'leaf' of length L for the condition of uniform heat flux, coincidentally yields an expression almost equal to (7) as $\mathrm{Nu} = 0{\cdot}679\ \mathrm{Pr}^{0{\cdot}33}\ \mathrm{Re}^{0{\cdot}5}$, with an equivalent expression for Sh (Sc, Re).

On the strength of the similarity between this latter expression and (7) it has been argued that results of flat-plate leaf studies should not differ significantly, whether they were obtained under conditions of uniform temperature (e.g. metal plates with high thermal conductivity) or uniform flux. However, leaves cannot be assumed to be adequately represented by rigid, flat plates in parallel flow, and local temperature distribution must be expected to reflect the complex pattern of BL thickness introduced by leaf morphology, surface structure or leaf motion (Fig. 1*b*). In such cases, a discrepancy in conduction may become a potential source of error (Vogel, 1984), particularly in situations where edge effects become important, as discussed below. Potentially significant differences ($\approx 20\%$) between uniform flux and uniform concentration (or temperature) have also been demonstrated for moisture transfer in forced convection (Takechi & Haseba, 1973) and calculated theoretically for heat transfer in free convection (Chen, Tien & Armaly, 1986*a*).

(*c*) *General description.* The bulk of leaf BL studies from the 1950s through the 1970s have been concerned with adaptation of flat-plate relationships for heat and mass transfer to conditions more or less representative of leaves in the natural environment. In general, results for forced convection have been expressed non-dimensionally by equations of the form

$$\mathrm{Nu} = c_{\mathrm{H}} \mathrm{Pr}^{0.33} \mathrm{Re}^{n} \quad \mathrm{Sh} = c_{\mathrm{M}} \mathrm{Sc}^{0.33} \mathrm{Re}^{n}. \tag{8}$$

The validity of the Re exponent $n = 0{\cdot}5$ in (8), as given by the Pohlhausen equation (7) for laminar BLs, has been widely confirmed for standard engineering shapes, in particular for heat transfer on flat plates at $\mathrm{Re} \leqslant 2{\cdot}5 \times 10^4$ (e.g. Sugawara *et al.*, 1958; Thomas, 1965), and at $\mathrm{Re} \leqslant 5 \times 10^4$ for plates with favourable pressure gradients (Kestin, Maeder & Wang, 1961). The $\mathrm{Re}^{0.5}$ relationship has been observed up to $\mathrm{Re} = 6 \times 10^5$ in pressure-stabilized BLs, such as in mass transfer from the forward-facing (stagnation) area of disks perpendicular to airflow, with $c_{\mathrm{M}} = 1{\cdot}08$ (Sogin, 1958). For leaves, free stream turbulence, shape and orientation are more likely to affect the constants c than the Re exponent n in the laminar range of BL flow. The 0·5 value for n has been confirmed at Re up to between 3×10^4 and 4×10^4 (Knoerr & Gay, 1965; Grace *et al.*, 1980). Appropriate constants c in (8) are usually determined empirically, often as enhancement factors in the form of multipliers α and β to account for effects of inclination and free stream turbulence, applied to the Pohlhausen value of $c_{\mathrm{H}} = c_{\mathrm{M}} = 0{\cdot}664$ for flat plates.

Upon transition from laminar to turbulent BL flow, the exponent n increases to 0·8 (Sugawara *et al.*, 1958; Thomas, 1965), with the following expressions proposed for local and average dimensionless heat transfer for horizontal flat plates with uniform surface temperature (Kreith, 1965)

$$\mathrm{Nu}_x = 0{\cdot}0288\, Pr^{0.33} Re_x^{\,0.8}$$

yielding

$$\mathrm{Nu} = 0{\cdot}036\, \mathrm{Pr}^{0.33}\, \mathrm{Re}^{0.8} \tag{9}$$

Again, values of the constants may differ for real leaves.

(*d*) *Transition to turbulence.* The 'critical Re-value' ($\mathrm{Re}_{\mathrm{crit}}$) for transition to turbulence in the BL flow depends on a number of factors and cannot be generally defined. In extremely stratified flow over smooth plates it may be delayed to $> 10^5$, but a more realistic expectation for $\mathrm{Re}_{\mathrm{crit}}$ is 2×10^4 (e.g. Monteith & Unsworth, 1990). This expected value is in approximate agreement with observations on flat, rectangular leaf models by Chen, Ibbetson & Milford (1988*a*), who noted transition initiated for Re between 1×10^4 and 3×10^4, although not yet completed at $\mathrm{Re} = 3 \times 10^4$. For leaves, or leaf models with more or less realistic shape, surface structure or motion, transition may occur at much lower values of Re, but observations differ. Based on measured velocity profiles in the leaf BL, Grace & Wilson (1976) judged BL instability on a *Populus* leaf to start at $\mathrm{Re} \approx 7200$ in a laminar free stream, but at $\mathrm{Re} \approx 1860$ in a turbulent stream (with Re based on leaf dimension). At $\mathrm{Re} = 7200$ a laminar sublayer could still be detected at 0·1 mm from the surface, but not at $\mathrm{Re} = 8800$. Grace (1978) deduced, from sensors attached to a real, fluttering leaf, that transition to turbulence occurred in laminar free stream flow at $\mathrm{Re} \approx 2{\cdot}3 \times 10^4$ (close to the expected value of 2×10^4 for flat plates), lowered to $\mathrm{Re} \approx 4000$ for turbulent flow. Considering that the BL over an extended leaf may contain both laminar and turbulent parts, some authors have proposed the use of an expression combining (7) and (9) (e.g. Kreith, 1965, p. 314; or first equation in (14)), but such expressions have not been widely used.

3. *Description of transfer in free convection*

Semi-empirical dimensionless expressions have been derived for leaf transfer in free convection in an analogous fashion, using the Grashof number Gr, as defined in (5), to characterize the intensity of buoyancy. Heat and mass transfer are then expressed in dimensionless relationships Nu (Pr, Gr) and Sh (Sc, Gr) as

$$\mathrm{Nu} = k_{\mathrm{H}} \mathrm{Pr}^{m} \mathrm{Gr}^{n} \quad \mathrm{Sh} = k_{\mathrm{M}} \mathrm{Sc}^{m} \mathrm{Gr}^{n} \tag{10}$$

Classical heat transfer analysis for smooth, vertical plates suggest $n \approx m = 0{\cdot}25$ with $k_{\mathrm{H}} \approx k_{\mathrm{M}} \approx 0{\cdot}5$ for $10^4 < \mathrm{Gr} < 10^9$ (Kreith, 1965; Schlichting, 1968, pp. 300–305). As with forced convection, values of the constants for standard shapes and orientations may be found in the literature (e.g. Monteith & Unsworth, 1990, Appendix A-5), with empirical adjustments required for more realistic leaf shapes. There is some uncertainty about lower limits of applicability (in terms of Gr) for the various proposed relationships (Dixon & Grace, 1983), because most experimental investigations do not cover the range below $\mathrm{Gr} \approx 10^4$, while Gr values for leaves in the natural environment may range as low as 10^2. The numerical analysis of Miyamoto *et al.* (1985), at any rate, suggests that (10), with $m = 0{\cdot}25$ and $k_{\mathrm{H,M}} \approx 0{\cdot}5$ (as above) and a constant addition of 0·448 to Nu, is applicable to vertical plates at $15 < \mathrm{Gr} < 2{\cdot}7 \times 10^4$. For horizontal plates in the same low range of Gr, the added constant would be 0·353 and values m and $k_{\mathrm{H,M}}$ would be 0·2 and 0·55, respectively.

4. *The characteristic length*

The definition of an appropriate 'characteristic dimension' L (to be used in Nu, Sh, Re or Gr) is

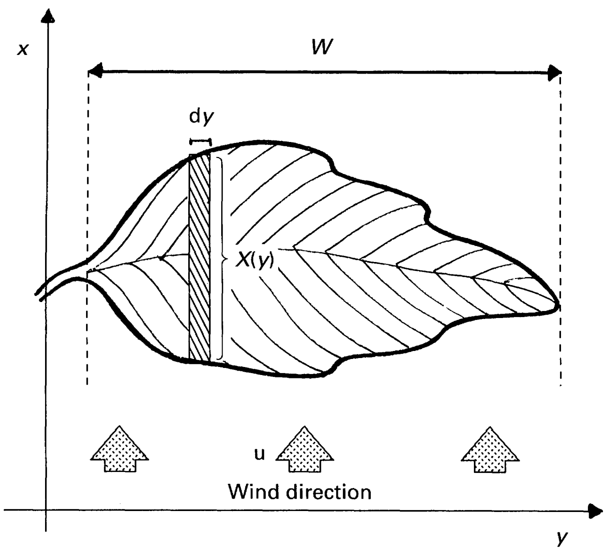

Figure 2. Schematic of leaf geometry, illustrating variables used in determination of characteristic leaf dimension.

relatively obvious for standard geometric shapes (length of plate, diameter of sphere or cylinder), but less so for leaves and plant elements with often irregular shapes. A physically meaningful definition should express the mean BL thickness in terms of a weighted mean distance from the leading edge. The most widely accepted formulation for the case of uniform surface temperature (Parkhurst, 1968) could be argued as follows (see Fig. 2): Considering that the local Nusselt number Nu_x ($= h_x x/\alpha$) at downstream distance x is proportional to $Re_x{}^n$, where Re_x is the local Reynolds number (ux/ν), the local transfer h_x along x varies as x^{n-1}. Integrated over each streamwise segment of length $X(y)$, the total transport from the segment is proportional to X^n, and the total leaf transfer proportional to the integral of X^n across the leaf of width W. Conversely, we may write the total leaf transfer according to (8) in terms of the characteristic dimension L (used in Nu and Re), in which case the leaf transfer is expressed as the product of a mean conductivity h, proportional to L^{n-1}, and leaf area given by the integral of $X(y)$ across the leaf width W. Since the proportionality constants are the same in each case, we can equate these expressions as

$$L^{n-1}\int_0^W X(y)\,dy = \int_0^W X(y)^n\,dy \qquad (11)$$

In laminar flow ($n = 0{\cdot}5$), the characteristic length would then be given by

$$L = \left[\frac{\int_0^W X(y)\,dy}{\int_0^W X(y)^{0{\cdot}5}\,dy}\right]^2. \qquad (12)$$

The formulation in (11) is also valid for turbulent flow ($n = 0{\cdot}8$) and for free convection (with $n = 0{\cdot}75$). Characteristic lengths L for most leaf shapes are typically between 0·5 and 0·8 of the maximum leaf dimension in the direction of flow (Parkhurst *et al.*, 1968). Alternatively, a characteristic length L could be defined as the square root of the one-sided leaf area (i.e. the side of a square with the same surface area as the leaf), with a shape factor which accounts for differences in leaf shape (Thorpe & Butler, 1977). All such definitions are physically inappropriate for highly dissected, three-dimensional leaf structures; in such cases effective characteristic dimensions may best be derived from observation of transfer, based on estimated surface area (Gurevitch & Schuepp, 1990).

The description of boundary layer resistance for sperhical plant parts has been reviewed by Nobel (1975). For nearly spherical objects, the diameter d of the sphere with equal surface area is chosen as the characteristic dimension. Dimensionless expressions for Nu(Pr, Sc) and Sh(Sc, Re) are as given in (8), with appropriate constants compiled in the reference literature (e.g. Monteith & Unsworth, 1990; Appendix A-5). Observed surface temperature excess of seed onion umbels over ambient air temperature, for example, which could conceivably lead to enzyme denaturation in onion seed, differed by up to a factor of five between 'loose' and 'tight' umbels (Tanner & Goltz, 1972). In the case of the former, L would be defined by the characteristic dimensions of structural elements within the umbel, while for the latter, L would correspond to the diameter of the approximately spherical umbel, with much greater BL thickness and correspondingly high temperature excesses.

The derivation of (11) (Fig. 2) treats each streamwise segment of the leaf as if it were part of an infinitely wide plate of equal streamwise dimension. In other words, it does not recognize edge effects, which must be expected to increase with increasing aspect ratio $AR = L/W$ (i.e. with decreasing width W), and with decreasing leaf size. Effects of aspect ratio, which are particularly important in inclined flow, will be discussed below (section V). Model simulations on horizontal flat plates suggested small edge effects ($< 10\,\%$) for leaves with size > 5 mm, particularly since the low conductivity of leaves makes transfer from the cooler edges relatively less significant (Chen, Ibbetson & Milford, 1988*a*), but the wavy and serrated edges of many real leaves make it difficult to draw general conclusions.

5. *Model types*

(*a*) *Physical models*. Much of our insight into leaf BLs derives from observations and simulations in systems that might appear abstract and artificial compared with natural leaves. Transfer processes from and to foliage in the natural environment are usually subject to simultaneous variation in wind, humidity, radiation, leaf motion, physiological parameters and possibly even microbiological factors, so that it is difficult to isolate effects of single parameters and to generalize observations. By contrast, the laboratory provides a controlled environment, and artificial leaves offer the advantage of known flatness, known radiative and thermal properties, and the convenience of a simplified energy balance either by suppressed transpiration of dry models or by elimination of stomatal effects in evaporation from model surfaces. Possible disadvantages resulting from the high thermal conductivity of metallic models have already been mentioned (section III.2*b*). It is possible to construct more realistic artificial models for transpiration studies, using teflon membranes or other porous material of low thermal conductivity (Morrison & Barfield, 1981), but subsequent development has generally favoured numerical leaf energy balance simulation, validated or complemented by selected field observations.

(*b*) *Numerical models*. Realization of the difficulties in interpreting leaf observations in the face of many interacting environmental and physiological variables on the one hand, and of the loss of realism in experimental simulations under controlled conditions on the other, coincided with the advent of widely available computing facilities for numerical simulation of leaf exchange processes. Whole-plant simulation models, unless very carefully adapted to the physiological and physical characteristics of a given plant and its environment, are as yet more likely to be of diagnostic than prognostic use. For example, simulations of the response of a plant to water stress may elucidate how the boundary layer component and the stomatal component contribute to species differences in simulated leaf conductance, sometimes in opposite directions (McCree, Fernandez & Ferraz-de-Oliveira, 1990). Regional models of moisture balance or photosynthesis are affected not so much by individual leaves as by their interaction and feedback mechanisms in the canopy environment. Leaf models are, therefore, often integrated as submodels in canopy models. For a review of earlier plant–atmosphere exchange concepts for photosynthesis, with consideration of leaf BLs, see e.g. Legg (1985). A brief discussion of some current models will be given in section IX.4.

IV. EFFECTS OF TURBULENCE ON IDEALIZED SHAPES

1. *Turbulence in canopy and leaf BL*

One of the most important determining factors for transfer across the leaf BL and, as a consequence, for the magnitude of the constants in (8), is whether the flow in the BL is laminar or turbulent. This, in turn, depends on the nature of the turbulence in the ambient air flow (free stream), on leaf shape and leaf motion.

Turbulent flow is characterized by significant fluctuations (u′) in the mean flow velocity u. It is often described by its intensity ($\mathrm{TI} = [(u')^2]^{1/2}/u$), i.e. by the square root of the velocity variance normalized with respect to mean velocity, and by its spectrum. The latter distributes the power in turbulent fluctuations among the various frequencies or spatial dimensions inherent in turbulent motion. Turbulence inside a plant canopy is physically inevitable for all but vanishing wind. It results from shear flow at the canopy top, intermittent incursions of 'turbulent structures' from the convective planetary boundary layer above the canopy and – in the case of thermal instability – from buoyant rising of warmer air parcels. Turbulence spectra in plant canopies show the effects of shear forces and wake flow from canopy elements (leaves, stems and trunks) superimposed on a complex cascade of disintegration of large atmospheric eddies into smaller ones (e.g. Baines, 1972; Finnigan & Raupach, 1987). Given the reduced wind speed in canopies, the TI is generally high, typically between 40 and 70% (Cionco, 1972). Discrepancies between results observed in different systems are often due to differences in turbulence characteristic, and differences in interactions of turbulence with different shapes, and have led to early scepticism with regards to laboratory simulations as a substitute for field observations (Philip, 1966).

While wind in a canopy is almost always turbulent, it is much harder to predict whether or not the flow in the leaf BL is laminar or turbulent (section III.2 *d*). Transition to turbulent BL flow is favoured by free stream turbulence, surface roughness or any other factor that could produce instability near the leaf surface. The observations by Grace & Wilson (1976) showed not so much a sudden instability as a gradually reduction of the laminar part of the BL into a progressively thinner laminar 'sublayer' with increasing Re. For this reason, most experimental studies in turbulent flow (as reviewed below) have suggested the broad validity of the (laminar) $n = 0{\cdot}5$ exponent in the Re-dependence (8) for leaves in 'canopy-like' flow situations, analogous to the Pohlhausen equation (7). The effects of turbulence are then expressed through adjustment of the constants c_H or c_M in (8). As will be shown later, the effect of free stream turbulence on a leaf strongly depends on its orientation against the direction of flow (inclination) and its aspect ratio.

2. *Model experiments*

The transfer-enhancing role of free stream turbulence has been well documented in engineering heat and mass transfer studies for bluff objects, such as inclined plates, cylinders or spheres, although reported effects differ widely. Unless otherwise indicated, the studies mentioned below involve wind tunnel observations in air. The majority of studies found that turbulence hardly changes the velocity dependence (Re-exponent), so that its effect could be satisfactorily expressed by a constant multiplier applied as an enhancement factor $\beta > 1$ to the previously introduced Nu(Pr, Re) or Sh(Sc, Re) relationships (see e.g. Kestin, 1966, for early, classical work on heat transfer to cylinders and spheres). Free stream turbulence may, however, lower the critical Re for transition from laminar to turbulent BL flow (section III.2*d*), at which point the Re-exponent will increase (9). Some authors found the turbulent Reynolds number Re_T, defined as the product of Re and TI (in absolute rather than percentage units), a useful parameter to delineate ranges of Re where turbulence has a significant effect on transfer (e.g. Gostkowski & Costello, 1970).

Studies on flat plates, aligned parallel to the flow, generally showed small enhancement (< 10%, i.e. $\beta < 1{\cdot}1$) for low TI in laminar BL flow with Re < 2×10^4 (Sugawara *et al.*, 1958; Thomas, 1965; Parkhurst & Pearman, 1974; Gostkowski & Costello, 1970; Chen *et al.*, 1988*a*). Significant (and highly divergent) effects were reported for higher values of TI and/or Re: Sugawara *et al.* (1958) found heat transfer increasing non-linearly by factors β of 1·08 to 1·65 when TI increased from 1 to 8·3% at Re values in the transition region to turbulent BL flow (Re > 30000). Enhancement of $\beta = 1{\cdot}65$ was also observed in heat transfer at a relatively low TI of ⩽ 3·8%, but at Re > 50000 in laminar flow stabilized by positive pressure gradients (Kestin *et al.*, 1961). This is comparable to the value of $\beta \approx 1{\cdot}5$ for vapour transfer from plates in the natural turbulence of a plant canopy found by Haseba (1973*a*). Chen *et al.* (1988*a*) suggested that their observed heat transfer increase of β between 1·1 and 1·5 at Re ≈ 20000 did not only depend on TI (which ranged from 5 to 25%), but also on the longitudinal integral scale of turbulence L_u, a measure of the longitudinal size of the energy-containing eddies in the flow (section IV.3). The very high enhancements (β between 2 and 3) observed in mass transfer (naphthalene) by Thomas (1965) at TI ≈ 13% might have been due partly to asymmetry in the flow channel, leading to flow separation at the leading edge.

Similar effects have been reported for the forward-facing 'stagnation' area of spheres, which are also characterized by laminar BLs: $\beta \approx 1{\cdot}17$ for TI ⩽ 12% at Re = 7200 (Sato & Sage, 1958), or β between 1·5 and 1·79 (depending on Re) at TI = 40%, with significant increase only when the turbulent Reynolds number Re_T (as defined above) exceeds 7000. The contrast between the small observed increase in heat transfer near the forward stagnation point of spheres ($\beta < 1{\cdot}12$ for TI < 9·4% at 19000 < Re < 62000), and the pronounced effects (β between 1·34 and 1·82, depending on Re) at the 120° wake position (Newman, Sparrow & Eckert, 1972), suggests that effect of free stream turbulence may depend strongly on its interaction with the separated flow in the wake. Data obtained for plates (leaves) in parallel flow will differ, therefore, from those obtained in inclined flow (section V).

A summary of these observations is included in Table 1.

Table 1. *Enhancement of transfer by free stream turbulence, in terms of a multiplier β applied to the constant c in the Nu (Pr, Re) or Sh (Sc, Re) relationships* (7). *H and V designate heat and vapour transfer, respectively*

Author(s)	Re	TI	β	Experimental details
Sugawara *et al.* (1958)	$> 3 \times 10^4$	1%-8·3%	1·08-1·65	H; flat plate, parallel flow, transition region
Sato & Sage (1958)	7200	12%	1·17	H; sphere in stagnation area
Sato & Sage (1958)	$\leqslant 1{\cdot}8 \times 10^4$	40%	1·65 (avg)	H; sphere in stagnation area
Sato & Sage (1958)	$< 2{\cdot}1 \times 10^4$	6%	1·4	H; sphere in stagnation area; frequ. 20 Hz
Kestin *et al.* (1961)	$> 5 \times 10^4$	3·8%	1·65	H; pressure-stabilized plate flow
Parlange *et al.* (1971)	$< 1{\cdot}6 \times 10^4$	n.a.	⩽ 2·5	H; leaf section in turbulent labor. flow
Pearman, Weaver & Tanner (1972)	$< 2 \times 10^4$	nat. turbul.	1·5	H; natural and artif. leaf models in the field
Schuepp (1972)	$< 2 \times 10^4$	4% + flutter	1·4	Electrochem. simul. on metal-plated leaves
Haseba (1973*a*)	$\leqslant 2 \times 10^4$	≈ 20%	1·5	V; plate placed in nat. canopy turbulence
Chamberlain (1974)	≈ 4000	nat. turbul.	1·25	Pb vapour to leaves in canopy
Parkhurst & Pearman (1974)	$< 2{\cdot}1 \times 10^4$	11%	1·3	H; plate in parallel flow; frequ. 10 Hz
Wigley & Clark (1974)	$< 1{\cdot}4 \times 10^4$	≈ 35%	≈ 2·5	H; leaf models in wind tunnel
Grace & Wilson (1976)	≈ 8000	> 25%	2·5	V; leaf in natural sea breeze
Murphy & Knoerr (1977)	< 6400	n.a.	1·5	H & V; tree leaves in environ. chamber
Chen *et al.* (1988*b*)	2×10^4	5%-25%	1·1-1·5	H; plate in parallel wind tunnel flow

3. *Effects of frequency and scale*

There is no question that powerful periodic disturbance of the BL, such as by acoustically driven pressure waves at scales comparable to time and space scales of BL flow, cause significant increase in transfer through periodic flow reversal at the plate (Feiler & Yeager, 1962). If frequency is high enough, the average heat flux can be several times higher than without oscillation, due to effects of fluctuating friction on energy dissipation (Ishigaki, 1971). However, such studies bear little direct relevance to the study of leaf exchange processes, at turbulence scales and intensities comparable to those found in the natural environment.

In most of the studies reviewed in section IV.2, the spectral characteristics of turbulence were not specified, undoubtedly contributing to observed discrepancies. Early engineering studies on relationships between turbulence scale and object dimension were contradictory: Van der Hegge Zijnen (1958) found β sensitive to the ratio of longitudinal integral scale of turbulence L_u to cylinder diameter, with maximum effect when velocity fluctuations matched eddy shedding frequencies. By contrast, Lavender & Pei (1967) found little effect of scale on the heat transfer from spheres and suggested the turbulent Reynolds number (R_T) as a better predictor for transfer enhancement. The response of flow around bluff bodies to free stream turbulence is complicated by the fact that TI may be the dominant factor in the forward-facing stagnation area, with scale relatively unimportant, while scale-dependent resonance interaction may occur in the separated wake flow (Kestin & Wood, 1971). A frequency-dependence with bias towards higher frequency was indicated for heat flow from inclined plates (Parkhurst & Pearman, 1974), with $\beta \approx 1{\cdot}3$ for TI $= 11\%$ at a frequency of 10 Hz, but $\beta \approx 1{\cdot}4$ (close to the maximum observed enhancement of 1·5) at a lower TI of 6% at 20 Hz. Assuming Taylor's hypothesis of 'frozen turbulence', i.e. translating frequencies into wavelengths through mean flow velocity, the shortest wavelengths in Parkhurst & Pearman's study would have slightly exceeded their plate length. An inverse relationship between the enhancement of transfer and the ratio of turbulence scale to plate length is also indirectly supported by Haseba (1981), who observed increases of $\beta \leqslant 2{\cdot}5$ in vapour transfer from oscillating 5 cm plates, at frequencies corresponding to eddy scales of the order of 4 cm at wind velocities of $\approx 0{\cdot}2$ m s^{-1}. This enhancement could be reduced by either decreasing frequency of oscillation or increasing velocity, and dropped to $\leqslant 1{\cdot}1$ at $u = 4$ m s^{-1}.

The relationship between longitudinal integral scale of turbulence (L_u) and streamwise plate length (L) has been further examined by Chen *et al.* (1988*a*). Plots of β *vs.* L_u/L showed monotonic decrease in heat transfer for parallel flow and for the upstream side of an inclined plate, for $L_u/L > 0{\cdot}1$, from a maximum value of β between 1·2 and 1·5, at TI of 11 and 20%, respectively. This suggests that the smallest eddies are the most efficient in penetrating laminar BLs. Chen *et al.* suggested that the ratio L_u/δ with δ the BL thickness, might be a better predictive parameter for β in such cases. On the downstream (wake) side of an inclined plate, maximum enhancement was $\beta \approx 2{\cdot}15$ at L_u/L of 0·5 and 0·9 for inclination angles of 20° and 90°, respectively (Chen, Ibbetson & Milford, 1988*b*). This clearly suggests a resonance effect between wake flow and free stream turbulence, reminiscent of the observations of van der Hegge Zijnen (1958). Table 1 includes the relevant data of this section, together with those obtained on leaf models and in canopy flow.

In summary, turbulence must be expected to affect transfer in parallel flow, or on the upwind side of an inclined leaf, when the most energetic eddies are small compared with the overall plate (leaf) length. On the downwind (wake) side of an inclined leaf, turbulence would be most effective when eddies are comparable to leaf dimension. Effects may be particularly pronounced in the transition region to turbulent BL flow. This suggests a potentially significant influence on transfer by turbulence produced in the wake of stems, leaves and other canopy elements. It also suggests that the absence of large scale eddies in wind tunnel simulations may not seriously affect the validity of conclusions, as has sometimes been feared (e.g. Philip, 1966). At very low frequencies, turbulence may be physically equivalent to a change in angle of attack of the flow, which generates its own associated effects on transfer (as discussed in section V).

V. EFFECTS OF ASPECT RATIO AND INCLINATION

1. *Eddy shedding*

Leaves are seldom aligned parallel to natural airflow so that effects of inclination on BL transfer must be addressed. Many studies on inclined surfaces are formulated for two-dimensional flow (streamwise direction and the direction perpendicular to the surface), assuming negligible gradients in the cross-stream dimension. In this case, heat and mass transfer for the upstream side of the ('infinitely wide') plate, facing into the wind at some angle of attack $\Theta > 0$, can be described by the so-called wedge-flow solutions (Kays, 1966). Their form is analogous to that given for flat plates in (8), with exponents $n = 0{\cdot}5$ and constants c_H or c_M dependent on Θ. No general analytical solution has been defined for the downwind surface, where the BL may separate from the plate due to adverse pressure gradients at higher angles Θ, with eddy shedding from the wake region (Fig. 3).

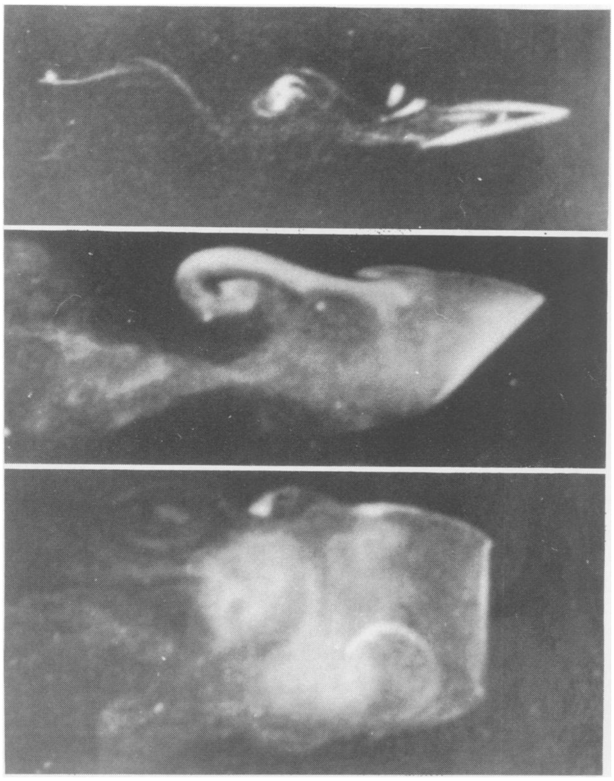

Figure 3. Visualization of flow behind plate inclined at angles Θ of 15°, 45° and 90°, at Re ≈ 650 (from Eden, 1912).

To understand effects of inclination on transfer, the flow separation at the leading edge of inclined plates must be considered. As shown already in the early visualizations of two-dimensional flow by Eden (1912) (Fig. 3), characteristic vortices appear in the wake flow at angles $\Theta > 10°$. The Strouhal number $S = nL \sin \Theta / u$ expresses eddy shedding frequency n non-dimensionally in terms of characteristic streamwise dimension of the plate (L), angle of attack (Θ) and free stream velocity (u). For Re values of interest to leaf transfer its magnitude is about 0·2 (Calvert, 1967), so that eddy shedding frequency behind a 5 cm leaf, inclined at 45° to wind of 1 m s^{-1}, would be ≈ 8 Hz. Further examination of the wake flow behind circular disks (Calvert, 1967) showed a reverse flow, generated by vortices formed at leading (and sometimes at trailing) edges. This reverse flow may converge on the plate for re-attachment or it may leave the plate, depending on Re (as seen in Figs 5 & 6). Calvert (1967) found the Strouhal number for disks (based on disk diameter) in agreement with that for squares of the same area (based on side length), suggesting some justification for using square plates as models for disks, if not leaves.

While we might not conceive of leaves in natural airflow as being sufficiently defined, as an experimental system, to exhibit vortex shedding with anything approaching the regularity observed in laboratory flows, eddy shedding is a real phenomenon, with associated potential consequences for leaves downwind of other leaves. Leaves also exhibit characteristic ratios of streamwise length L to cross-stream width W (aspect ratio $\mathrm{AR} = L/W$). Since the effect of inclination strongly depends on aspect ratio, the two factors will be discussed together. Effects of inclination (at angle Θ) will be expressed by the ratio of mean transfer coefficients $\alpha = h(\Theta)/h(\Theta = 0)$, either for the whole plate (leaf) or for each of its sides.

2. *Model experiments*

(*a*) *Observations.* Unless stated otherwise, the results reviewed below have been obtained for $4 \times 10^3 < \mathrm{Re} < 8 \times 10^4$, i.e. in the Re range most relevant to leaf transfer. In some cases, observations represent an average over a number of Re values within that range.

Studies of the upstream (forward-facing) side of plates show the general characteristics of a pressure-stabilized laminar BL, with modest increase in heat or mass transfer over the predictions of the Pohlhausen equation (7). The transfer enhancement $\alpha = h(\Theta)/h(\Theta = 0)$ increases non-linearly from 1 to between 1·2 and 1·4 (see Fig. 4*a*) as the angle of attack Θ increases from 0° to 90° (e.g. Powell, 1940; Haseba, 1973*b*; Parkhurst & Pearman, 1974; Chen, Ibbetson & Milford, 1988*b*). Transfer enhancement with inclination on the forward surface, due to compression of BL thickness, is always observed unless flow separation at a blunt front edge causes a recirculating bubble (Motwani, Gaitonde & Sukhatme, 1985).

By contrast, the downstream (wake) side exhibits complex enhancement peaks (α_{max}) and reduction patterns as a function of Θ, strongly dependent on aspect ratio (AR) (Figs 4*a* and *b*). Powell's (1940) data on evaporation of water from filter paper on rectangular plates of approximately uniform surface temperature, for $0{\cdot}2 < \mathrm{AR} < 1{\cdot}4$, showed highest values of α_{max} (≈ 2·06) for AR = 1·4 at $\Theta \approx 40°$ (Fig. 4*b*). A comparison of Powell's observed α_{max} of 1·95 at $\Theta = 30°$ for square plates (AR = 1) against Haseba's (1973*a*) data on evaporation from circular disks ($\alpha_{max} \approx 1{\cdot}8$ at $\Theta = 16°$), or against Chamberlain's (1974) mass (Pb vapour) transfer data from circular disks ($\alpha_{max} \approx 1{\cdot}5$ at $\Theta = 20°$), illustrates the variability of empirical results. The study of evaporation from square plates by Chen *et al.* (1988*b*) found α_{max} of 1·7 and 1·9 (for Re 1×10^4 and $2{\cdot}1 \times 10^4$, respectively, at 20°, decreasing to < 1 for angles between about 33° and 80° (Fig. 4*a*). Triangular or sinusoidal serration at the leading edge of the plates did not increase transfer significantly at angles Θ near peak effectiveness (≈ 20°), nor at high angles of incidence with separated wake flow, but caused a pronounced increase (from $\alpha = 1$ to $\alpha = 1{\cdot}4$) at low Θ through a broadening of the enhancement peak. This agrees qualitatively with Vogel's (1970) observations

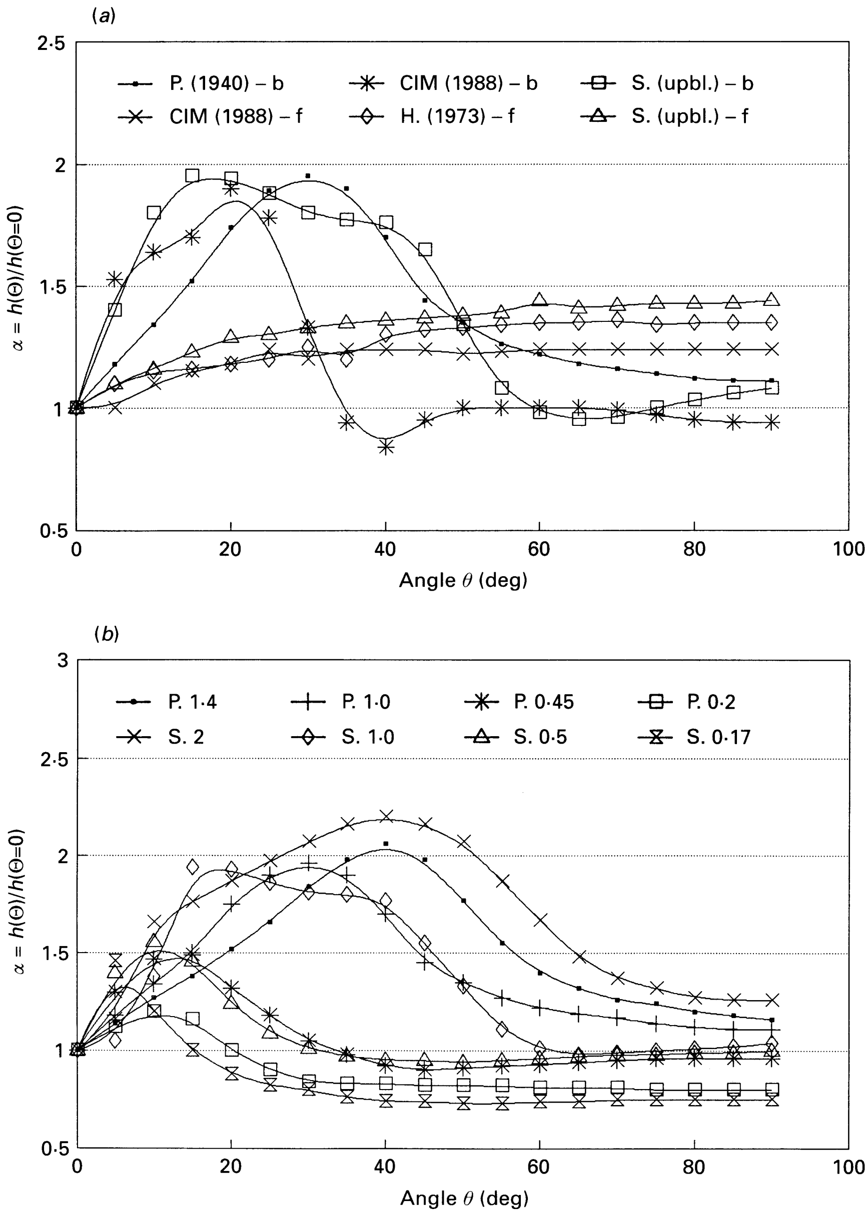

Figure 4. Effects of aspect ratio (AR) and inclination Θ: (*a*) data for front (–f) and back (–b) for AR = 1 from Powell (P) (1940), Haseba (H) (1973*b*), Chen, Ibbetson & Milford (CIM) (1988*a* and *b*), and electrochemical simulations by the author (S) (unpublished); (*b*) data from Powell (P) (1940) and the author (S) (unpublished) for AR between 2 and 0·17.

that irregular shapes not only enhance transfer over circular plates in bluff flow, but make the enhancement less dependent on angle.

A selection of empirical data obtained in various systems for AR = 1 on front (f) and back (b) of inclined plates (Fig. 4*a*), and for AR between 2 and 0·17 for the back of inclined plates (Fig. 4*b*), illustrates the general features of *AR*-related effects. Haseba & Ito (1980 and 1984), on the basis of their evaporation measurements from rectangular plates in a wind tunnel for 0·05 < AR < 50, summarized them by stating that α increases with streamwise dimension for plates with fixed cross-stream width, and decreases with increasing width for plates with fixed streamwise length. It is not surprising that enhancement is most pronounced – and extends over a wide range of angles – for surfaces with high value of AR, i.e. with pronounced streamwise dimension. In this case, the laminar BL in parallel flow develops significant thickness, with correspondingly high BL resistance, and the disturbance introduced by recirculating turbulence from separation at the leading edge will be highly effective. At what angle enhancement decreases, often falling below 1, depends on whether recirculating eddies are connected to the surface or not, as discussed in section V.2*b*.

A number of studies reported the total two-sided transfer: Parkhurst *et al.* (1968) found $\alpha \leqslant 1{\cdot}83$ in total heat transfer from inclined metallic ellipses with varying degrees of eccentricity. Maximum

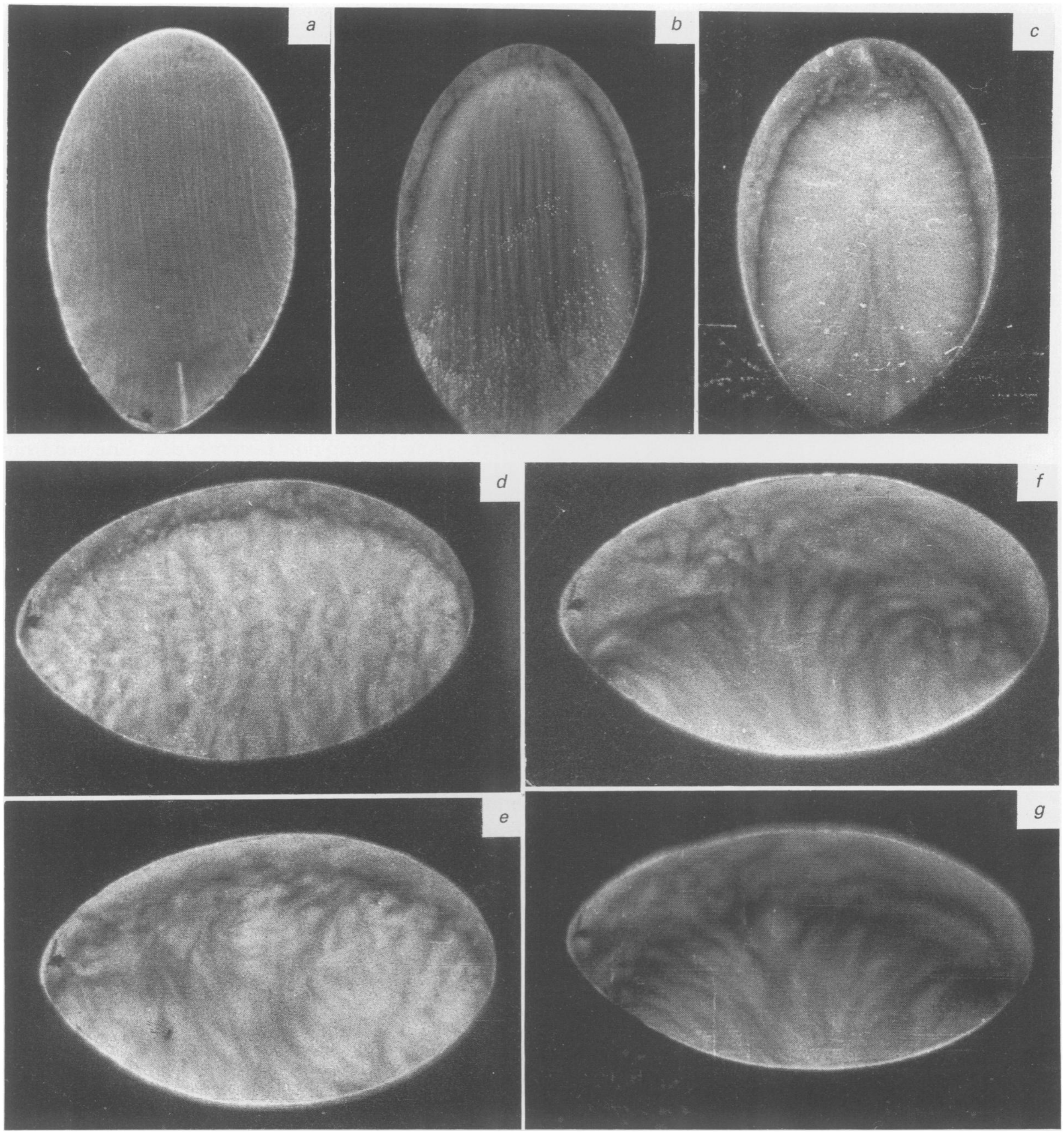

Figure 5. Electrochemical visualization of transfer (by the author) at the downstream (wake) side of inclined elliptical plates, with flow (from the top) along and across the major axis at Re $\approx$ 1100. Angles of attack Θ are: (*a*) 0°; (*b*) 5°; (*c*) 30°; (*d*) 5°; (*e*) 10°; (*f*) 20°; (*g*) 45°. Recirculating flow is connected to the surface in (*c*), but not in (*f*) or (*g*). AR is 1·8 in (*a–c*) and 0·56 in (*d–g*).

effect was observed for the most elongated ellipse, with axes AR of 7·2, at $\Theta = 60°$. Given the relatively weak effect of inclination at the upstream side, it is not surprising that such data tend to be dominated at lower angles Θ by the prominent increases on the wake side. At higher angles, the relative decrease on the wake side is compensated by the gradual increase in transfer on the front. Chen *et al.* (1988*b*) documented the dependence of heat and mass transfer from inclined square plates on turbulence characteristics. Increases in TI from 3·5% to 20% produced increased transfer at inclinations where transfer was low (such as at 90° in the wake flow), but negligible effects at inclinations with high values of α.

Parkhurst & Pearman (1974) eliminated edge effects (by spanning the width of the flow channel with a rectangular heat transfer plate). While increases over the Pohlhausen expectation were small for parallel flow (turbulent enhancement $\beta < 1·2$ at all turbulence levels), inclination by as little as 4° to 8° increased enhancement up to factors between 1·3 and 1·5, with subsequent decrease for $\Theta > 8°$, in general agreement with the data for small AR in Fig.

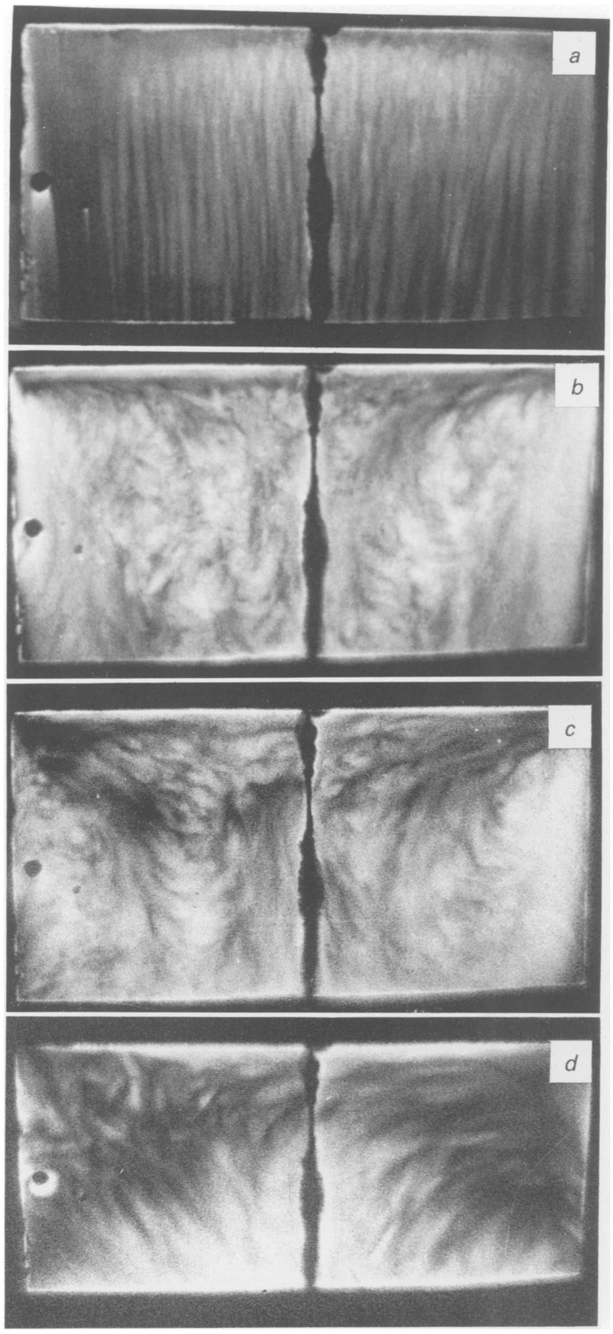

Figure 6. Electrochemical visualization of transfer (by the author) at the downstream (wake) side of a rectangular plate with AR = 0·5 (flow from the top), at Re ≈ 1200. Angles of attack Θ are: (*a*) 0°; (*b*) 5°; (*c*) 15°; (*d*) 45°. Recirculating flow is connected to the plate in (*b*) and (*c*), but has moved off the plate in (*d*). (The dark band along the centre transect results from a locally non-conducting joint).

4*b*. The fact that this enhancement remained at ⩾ 1·4 up to Θ ≈ 75° in the presence of free stream turbulence, with TI = 6 % at a frequency of 20 Hz, again suggests an effective potential interaction between free stream turbulence and wake flow.

(*b*) *Visualizations*. Effects of aspect ratio (AR) and inclination must be interpreted in terms of the recirculating separated flow. This is shown qualitatively in Figs 5 and 6 by electrochemical flow visualizations on the downstream surface of inclined rectangular and elliptical plates (Schuepp, unpublished). Bright areas indicate high transfer, i.e. compressed BL thickness, resulting from turbulent agitation near the surface. At zero incidence, the generally increasing BL thickness can be seen as a gradual darkening of the downstream areas. The BL instability introduced even at small angles (5°) is evident in both Figures, explaining observations such as those of Parkhurst & Pearman (1974) mentioned above. At angles of 10 to 15 degrees, a strong recirculating flow tends to provide areas of high transfer near the downwind edge of the plates. In cases of small AR (crossflow images in Fig. 5; Fig. 6), the recirculating flow becomes disconnected from the plate at angles around 20°, causing the drop in transfer with higher values of Θ. In the case of high AR, such as for the ellipse with flow along the major axis (Fig. 5, top), the recirculating flow remains connected to the plate, causing effective enhancement at higher values of Θ.

(*c*) *The Re exponent*. Observations on bluff bodies (including inclined plates), with flow separation in the wake region, often reported changes in velocity dependence of transfer, i.e. in the Re exponent of the Nu(Pr, Re) or Sh(Sc, Re) relationships (8). Deviations from the 0·5 exponent of the Pohlhausen equation (7) were usually insignificant for the upstream surface of inclined plates which maintains a pressure-stabilized laminar BL. For example, although Powell's (1940) data on evaporation from the front surface of disks at Θ = 90° were summarized as $Sh = 0{\cdot}625\, Pr^{0{\cdot}33} Re^{0{\cdot}56}$, they lie generally within 5 to 10 % of Sogin's (1958) data which document the general validity of the $Re^{0{\cdot}5}$ relationship (section III.2*c*). Such differences could be ascribed to experimental uncertainty. Increased Re exponents were observed, however, for the total transfer of inclined plates, due to enhanced velocity dependence of the separated wake flow. Reviewing early literature data, Richardson (1963) proposed an exponent of 0·66 for the separated flow region in the wake of a cylinder in crossflow. This agrees e.g. with Haseba (1973*b*) who found Re-exponents between 0·6 and 0·7 at angles between 10° and 20° for evaporation from inclined, flat plates. Overall transfer from both sides in inclined flow may, therefore, be characterized by an exponent n (8) which exceeds the Pohlhausen value by not more than 10 %.

Potential changes in the Re exponent, associated with clustering of leaves, will be discussed in section VI.3.

VI. LEAVES OR LEAF MODELS IN FORCED CONVECTION

1. *Velocity and humidity profiles in the BL*

There exist relatively few direct observations within leaf BLs that could be cited to validate the concepts reviewed above. The basic fact that BL thickness varies with leaf structure, with reduced thickness in deeply lobed leaves with smaller average distances from leaf edges than regular leaf shapes, has been documented by Baker & Myhre (1969). Yabuki, Miyagawa & Ishibashi (1970) confirmed leaf BL thickness as an increasing function of downwind displacement and a decreasing function of free stream velocity. Perrier, Aston & Arkin (1973) compared BL structure, in terms of wind profiles, friction forces and estimated turbulent diffusivity, between a real (slightly cupped) soybean leaf (*Glycine max* (L.) and a rectangular, smooth artificial leaf. Effects of curvature and roughness can be seen at all but the lowest ($0{\cdot}39\ \mathrm{m\,s^{-1}}$) wind speeds, with indication of earlier transition to turbulence (at $\mathrm{Re} < 1{\cdot}1\times 10^4$) for the rougher natural leaf. The sensitivity of surface BLs to disturbances induced by surface roughness is no surprise (e.g. Schlichting, 1968, pp. 610–623). Perrier *et al.* (1973) suggested, therefore, that a friction velocity (or some other measure of surface roughness) should be used as a scaling factor in studies on artificial leaves.

Wigley & Clark (1974) emphasized the increased heterogeneity in surface temperature distribution for a real *vs.* an idealized leaf (see Fig. 1*b*). The velocity profiles of Grace & Wilson (1976) and Grace (1978) on a *Populus* leaf (Fig. 1*a*) also documented the lowering of the critical Re value ($\mathrm{Re_{crit}}$) for transition from laminar to turbulent BL flow relative to that observed in engineering flat-plate studies, particularly in turbulent free streams (sections III.2*d* and IV.1). The proportionality between vapour density difference across the leaf BL and transpiration rate, with the proportionality constant dependent on air currents, and the dependence of vapour density and temperature profiles on both sides of leaves on free stream turbulence, have been directly confirmed by Kitano & Eguchi (1987).

2. *Observations of transfer*

Observations on real leaves, manipulated sections of leaves, and leaf models that aspire to some resemblance of leaf morphology, surface structure or motion, generally still contained elements of artificiality, most often in their effort to eliminate stomatal exchange as a variable. Whenever BL conductance (or resistance) was the primary object of study, temperature or concentration difference across the BL had to be well defined. This often meant the use of surrogate leaves, with associated problems in surface boundary conditions (e.g. uniform temperature *vs.* uniform flux) as already discussed. As a consequence, the dividing line between them and the more 'abstract' plate models (sections IV and V) is not sharply defined. In general, leaves or leaf models enjoy an advantage of greater realism, often at the expense of precision in the definition of geometry or flow conditions. Plate model simulations often helped to interpret results of leaf and leaf model studies and observations from both should be seen as complementary in defining expectations – and interpreting observations – for transfer from real leaves.

Similar to the objectives of the preceding sections, the studies reviewed here attempted to define the constants n, c_{H} and c_{M} in (8) for leaves in natural conditions, either directly or through an enhancement factor β over expectations for smooth, flat plates.

Very high enhancements of $\beta \leqslant 2{\cdot}5$ over the Pohlhausen equation (7) were reported by Parlange, Waggoner & Heichel (1971) for heat transfer from tobacco leaf sections in turbulent laboratory flow of unstated TI, under conditions of suppressed transpiration. Effects of leaf curvature appeared to be slight and flapping (at a frequency of 4 Hz and amplitudes of 12 cm) produced no further enhancement. While this high value of observed transfer may have been partly attributable to experimental factors (vorticity in turbulent flow created by the rotary fan, causing non-parallel flow at the plate, or inadequate surface temperature measurements by thermocouples not integrated into the leaf surface) their observations raise the question of 'saturation' i.e. a maximum degree of BL disturbance beyond which further agitation will not result in further increase in transfer. The concept of a saturation value appeared to be qualitatively confirmed in a follow-up study on reed (*Phragmites communis*) leaves in a sea breeze (Parlange and Waggoner, 1972). Grace & Wilson (1976) found enhancement rates comparable to those of Parlange *et al.* (1971) in transpiration from a *Populus* leaf. This enhancement was, surprisingly, not strongly dependent on TI, which varied up to 25%. The high value of $\beta \approx 2{\cdot}5$ could not be explained by the error analysis presented by these authors.

The studies just described contrast in their high projected enhancements over the Pohlhausen equation with a number of studies that found $\beta < 2$, with an average expected value around 1·5: Pearman, Weaver & Tanner (1972) examined heat transfer of natural and artificial leaves under field conditions. Their data could be expressed by best-fit regression as $\mathrm{Nu} = 1{\cdot}29\ \mathrm{Pr}^{0{\cdot}33}\mathrm{Re}^{0{\cdot}48}$, which differs non-significantly from $\mathrm{Nu} = 1{\cdot}08\ \mathrm{Pr}^{0{\cdot}33}\mathrm{Re}^{0{\cdot}5}$, equivalent to an increase of $\beta \approx 1{\cdot}5$ over the Pohlhausen equation. This expression agrees fairly closely with the data of Monteith (1965) ($c_{\mathrm{H}} \approx 1{\cdot}13$) when expressed correctly for surface area, as well as those of Raschke

(1956). Edge effects appeared to be negligible, i.e. results depended only weakly on absolute model size. A similar enhancement factor (average $\beta \approx 1{\cdot}4$) was observed in electrochemical simulations of transfer, under conditions of diffusion-dominated ion transport, on fluttering rectangular leaf-shaped plates and metal-plated real leaves, by Schuepp (1972). The difference between these observations and the value of β of about 1·25 found by Chamberlain (1974) on mass transfer (Pb vapour) to bean leaves in a canopy could probably be explained by differences in surface roughness, free stream turbulence and/or leaf motion. In controlled, ventilated environment chamber observations, Murphy & Knoerr (1977) calculated simultaneous heat and mass transfer coefficients for various tree leaves from measured leaf temperature, evaporation and environmental parameters. Results confirmed the validity of the Pohlhausen equation with enhancement factor $\beta \approx 1{\cdot}5$. For the turbulent region, the Re exponent of 0·84 suggested by Wigley & Clark (1974) (see below) was a good approximation. The suggested relationships were $Nu = 1{\cdot}0\, Pr^{0{\cdot}33}Re^{0{\cdot}5}$ for $Re < 7000$ and $Nu = Pr^{0{\cdot}33}[8{\cdot}96 + 0{\cdot}044\, Re^{0{\cdot}84}]$ for $Re > 7000$, with equivalent expressions for Sh(Sc, Re). Table 1 includes results given here, in terms of empirically observed enhancement over the predictions of the Pohlhausen equation.

Model experiments on aspect ratio and inclination (section V) were qualitatively confirmed by Harazono & Yabuki (1985) on inclined cucumber leaves ($10° < \Theta < 30°$) in laminar flow. Dry matter production, transpiration and photosynthetic rate were found to increase by factors α of between 1·1 and 1·38 over their values in parallel flow, with maximum enhancement at $\Theta = 20°$.

Unlike the studies mentioned above, which expressed transfer enhancement over the Pohlhausen equation by an approximately constant multiplier α or β, Wigley & Clark (1974) found their high turbulence (TI 30 % to 40 %) data on heat transfer at $Re < 1{\cdot}4 \times 10^4$ from leaf models of *Phaseolus* best represented by a local Nusselt number of $Nu_x = 0{\cdot}045\, Pr^{0{\cdot}33}Re_x^{0{\cdot}84}$. This represents a significant enhancement over smooth plate expectations (9), corresponding in magnitude (but not in Re-dependence) to that given by Parlange *et al.* (1971). Postulating possible deviations from the Pohlhausen equation even at $Re < 10^4$, Wigley & Clark did not recommend the use of β.

Some of these relationships are shown in Figure 7 which could be said to summarize a consensus of expectation on leaf transfer for single leaves: enhancement by an approximately constant factor of between 1·4 and 1·5 over the Pohlhausen expectation in the laminar range, with uncertainty as to when transition to turbulence in the BL occurs. At that point, we have to expect the associated change of velocity dependence, with higher Re-exponent.

While this review focuses on contiguous leaves, leaf studies need not be confined to such shapes. In electrochemical simulations with metal-coated leaves of various populations of the highly dissected *Achillea lanulosa* by Gurevitch & Schuepp (1990), leaf structure, including microscopic surface hairs, was left largely intact. The leaves showed high transfer conductances, in agreement with predictions of boundary layer theory for cylinders in crossflow, with characteristic dimensions comparable to the diameter of individual leaf subelements. Conductances tended to be greater, and L smaller, for the larger and more open leaves of a lower altitude

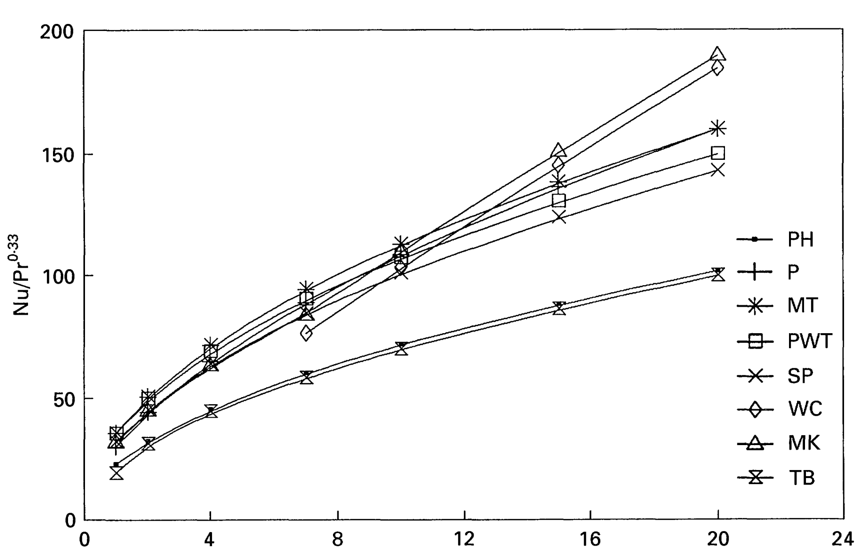

Figure 7. Dimensionless representation of transfer, as a function of Reynolds number (Re), from the following sources: PH, Pohlhausen equation (PH); P, Powell (1940); MT, Monteith (1965); PWT, Pearman, Weaver & Tanner (1972); SP, Schuepp (1972); WC, Wigley & Clark (1974); MK, Murphy & Knoerr (1977); TB, Thorpe & Butler (1977) (for sheltered orchard leaves).

population in contrast to leaves from high altitude plants, perhaps linked to morphological adaptation to local microclimates (see section VIII.3).

Very few systematic studies have been directed at leaf curvature. Thom (1968) found α_{max} of only 1·15 in one-sided vapour transfer from a slightly cusped, metallic artificial leaf in the approximate shape of broad bean (*Vicia faba*), for inclinations of 23° and 90°. Both, convex and concave surfaces were examined in orientation against the flow, and transport from the convex surface exceeded that from the concave one at all angles by about 20%. Results in parallel flow could be expressed by a 6% enhancement over the predictions of the Pohlhausen equation (7), which may be attributed partly to changes in effective dimension. These results do not preclude the possibility of a larger increase at some intermediate angle Θ, which might have been missed in an experiment that observed only one value of Θ between 0° and 90°.

3. *Aerodynamic interference*

The expressions discussed so far have been formulated for isolated leaves exposed to a more or less well defined free stream. As the number of leaves in any given volume increases, mutual aerodynamic interference between leaves tends to decrease transfer by a 'shelter factor' (p), resulting from reduced exposure to the free stream velocity (Landsberg & Thom, 1971; Thom, 1972). This may be counteracted, to some degree, by the action of turbulence produced by shear and pressure forces in the wake of canopy elements.

Landsberg & Thom (1971) derived shelter factors p_d and p_s for the transfer of momentum (drag forces) and scalars (heat or mass) from spruce shoots as $p_d = p_s = 1{\cdot}96\ \sigma^{0{\cdot}43}$, where σ is defined as shoot density (projected area of needles divided by projected area of the shoot). Similarly, Landsberg & Powell (1973) determined p_d and p_s (for water vapour) for natural and artificial apple leaves with various densities, defining foliage density as the ratio of the sum of projected leaf and stem areas over the frontal area of the tree. Since aerodynamic effects on bluff bodies involve pressure forces in the wake that have no equivalent in the transfer of scalars, p_d and p_s cannot in general be expected to be the same. The expression for the shelter factor for scalars proposed by Landsberg & Powell (1973) is

$$p_s(u, \sigma) = 0{\cdot}81\, u^{0{\cdot}12} \sigma^{0{\cdot}56} \tag{13}$$

with u the external wind speed. Typical values ranged from 1·3 to 1·8 (for wind speeds between 1 and 4 m s^{-1} and leaf densities between 2 and 3·2). This means that mutual interference would reduce transfer per unit leaf area by factors between 1·3 and 1·8 relative to that of isolated leaves in the same wind condition. In general, shelter factors implicitly assume random distribution of foliage elements and ignore effects such as flow channelling, which can lead to more specific local aerodynamic effects (Schuepp, 1989).

Thorpe & Butler (1977) examined heat transfer from real orchard leaves under natural conditions of sheltering and turbulence, but with artificially eliminated transpiration. Their results could be expressed by the best fit relationship $\mathrm{Nu} = 0{\cdot}46\,\mathrm{Pr}^{0{\cdot}33}\mathrm{Re}^{0{\cdot}54}$ (also included in Fig. 7), which compares well with the expression of Landsberg & Powell (1973) for the given porosity of the foliage. Discrepancies with other researchers could tentatively be ascribed to differences in the balances between sheltering and agitation (turbulence) in the various experiments.

VII. LEAVES AND LEAF MODELS IN MIXED AND FREE CONVECTION

1. *The transition regime*

Conditions of negligible wind (free convection) have been considerably less extensively studied than those of forced convection, which is perhaps surprising given the importance of greenhouse cultivation. Even fewer are studies in the transition region between forced and free convection, and a satisfactory description of the highly complex buoyancy effects in mixed convection on leaf boundary layers remains a challenge (Kitano & Eguchi, 1990). The relative paucity of empirical studies may result from a perception that conditions of very low wind may be rare in the natural environment, but it is precisely under such conditions that lethal temperatures are most likely to occur. Criteria have been developed to distinguish between free and forced convection on the basis of the $\mathrm{Gr}/\mathrm{Re}^2$ ratio, i.e. the ratio of buoyancy to friction forces. The transition region of 'mixed convection', however, is not sharply defined; semi-empirical criteria set the limits for 5% departure from pure free or forced convection at $0{\cdot}1 < \mathrm{Gr}/\mathrm{Re}^2 < 16$ (Parkhurst, 1968). A more complete, theoretical analysis by Chen, Armaly & Ramachandran (1986*b*) generalized such criteria for vertical and horizontal plates and proposed $0{\cdot}07 < \mathrm{Gr}_x/\mathrm{Re}_x^{\,2} < 7{\cdot}5$ as a more appropriate limit for the 5% departure on vertical plates, at the 0·7 value for Pr appropriate to heat transfer in air, and $0{\cdot}05 < \mathrm{Gr}_x/\mathrm{Re}_x^{\,5/2} < 9{\cdot}5$ for horizontal plates, where the subscript x again denotes local values of the similarity numbers. Using such criteria, a 5 cm leaf with a 10 °C temperature excess over ambient air would find itself in a mixed regime for wind speeds between 3 and 40 cm s^{-1}, which would not be uncommon in lulls between stronger wind or in sheltered habitats near the ground.

Traditionally, transfer in mixed convection has been determined by calculating Nu (or Sh) for both forced and free convection ((8) and (10)), then choosing the larger of the two. Alternatively, the sum of the conductances calculated for free and forced conduction may be used, equivalent to treating resistances due to the two convection regimes in parallel (Silva, Rosa & Candeias, 1988). Detailed analysis of data from flat, horizontal plates from a variety of sources (as reviewed by Foster & Smith, 1986) suggests the following expressions for Nu (and by analogy Sh) in the transition region

$$\left.\begin{aligned} \mathrm{Nu}^2_{\mathrm{forced}} &= \mathrm{Nu}^2_{\mathrm{laminar}} + \mathrm{Nu}^2_{\mathrm{turbulent}} \\ \mathrm{Nu}^{3\cdot5}_{\mathrm{total}} &= \mathrm{Nu}^{3\cdot5}_{\mathrm{free}} + \mathrm{Nu}^{3\cdot5}_{\mathrm{forced}} \end{aligned}\right\} \tag{14}$$

The maximum effect of buoyancy on forced convection from flat plates, at $\mathrm{Pr} = 0{\cdot}7$, would be an enhancement of $\approx 22\%$, according to the numerical analysis of Chen *et al.* (1986*b*).

The laboratory data on moisture transfer from simulated leaf models of two different sizes by Foster & Smith (1986) indicate that mixed convection, defined as the region of flow where $\mathrm{Nu}_{\mathrm{total}}$ exceeds $\mathrm{Nu}_{\mathrm{forced}}$ by $> 10\%$, extends typically to about $20\ \mathrm{cm\ s^{-1}}$ for the 10 cm leaf, or up to $\mathrm{Re} \approx 1300$. Simulated transpiration from hypo-, hyper-, and amphistomatous leaves show either increase or decrease with decreasing wind velocity, depending on feedback through changes in surface temperature, and its effect on vapour pressure depending on stomatal status. This can lead to some counter-intuitive predictions on potential effects of stomatal distribution as an evolutionary adaptation to sunny and shaded habitats (Foster & Smith, 1986).

2. *Observations of transfer*

The heat transfer studies of Vogel (1970), on variously shaped metallic models with non-uniform surface temperature, showed shape- and orientation-dependent wind effects under conditions of free and mixed convection. Wind of $0{\cdot}1\ \mathrm{m\ s^{-1}}$ and $0{\cdot}3\ \mathrm{m\ s^{-1}}$ increased transfer by factors of 1·1 to 1·4 and 1·3 to 1·95, respectively, over the no wind case. Effects were higher for the leaf models than for any of the abstract shapes. This illustrates the significant potential effect of small breezes in still air. In free convection, rotation from horizontal to vertical position increased total heat transfer by a factor of 1·26 for the circular plate, but only 1·04 to 1·14 for the irregular (deeply serrated) shapes. Electrochemical simulations on rectangular plates and metal-coated leaves (Schuepp, 1973) resulted in increases by factors of about 1·25 each for orientation and roughness effects. The maximum transfer of a rough, tilted leaf did not exceed that of a smooth vertical plate by more than a factor of 1·5. 'Hot-up' simulation exceeded 'hot down' on a horizontal leaf by a factor of about 3. Schlieren-type flow visualizations suggested that small scale surface roughness increases transfer by facilitating BL separation from the surface, especially for horizontal and tilted leaves (Schuepp, 1973), but such roughness effects may not be equally pronounced at high values of Gr where roughness and/or of serrated margins may delay transition to BL turbulence by stabilizing BL flow. Dixon & Grace (1983) report an extensive series of heat transfer observations from uniformly heated metallic leaf models in free convection. The agreement between calculated (Equation 10, with $n = m = 0{\cdot}25$ and $k_{\mathrm{H}} \approx 0{\cdot}5$) and observed values was good only for $\mathrm{Gr} > 10^5$. For smaller values of Gr, n varied between 0·1 and 0·2, with coefficients k_{H} between 1 and 2, so that values observed with decreasing Gr progressively exceeded the calculated ones. This agrees with earlier findings of Knoerr & Gay (1965), and is most likely attributable to edge effects, possibly exaggerated by the high thermal conductivity of the model leaves.

Oscillations ($\leqslant 5$ Hz) in free and mixed convection may not be common in natural system but would be very effective in disturbing the free convection BL, with associated increases in vapour transfer of rectangular plates up to factors of 5 (Haseba, 1981).

VIII. INTERPRETATION OF LEAF SHAPE

1. *Shape and size*

(*a*) *Description of shape.* The objective description of leaf shape remains a problem since a characteristic dimension based on engineering usage (as defined in section III.4) proves inadequate for complex leaves and clusters of leaves. More or less objective criteria can be developed to determine when shapes of flat leaves are 'significantly different', based on digital pattern analysis, such as the use of Fourier series to describe position vectors of leaf outline (Kincaid & Schneider, 1983). The full impact of the current explosion of fractal models and computer-based neural network techniques for the description of complex shapes cannot yet be assessed (McCord-Nelson & Illingsworth, 1991), but leaf categorizing algorithms have been developed for demonstration purposes (e.g. NeuralWare, 1991). In cases of finely dissected, three-dimensional leaf structure, experimental determination of an effective characteristic dimensions may be the most promising approach to derive BL thicknesses (Gurevitch & Schuepp, 1990, section III.4).

Undulations of leaf margins have been largely overlooked in the description of leaf morphology and its effect on BL transfer. It may not only account for some of the differences observed between experiments, but also between results from replicate models or leaves (Parlange & Waggoner, 1972; Gottschlich & Smith, 1982).

(*b*) *Sun-shade dimorphism.* Differences in morphology between leaves from different parts of trees or different habitats, in particular between sun- and shade leaves, have long been noted (Hanson, 1917). Sun leaves are generally smaller, thicker and more deeply lobed than shade leaves, resembling leaves from a dry habitat. Some similarities between sun-shade and drought tolerant-intolerant dimorphism have also been noted in anatomical and physiological factors of many species (Ashton & Berlyn, 1992). The fact that sun leaves tend to possess higher stomatal density makes it unlikely that their morphology evolved primarily as a response to water scarcity (Vogel, 1968). Considering the fact that a broad leaf in bright sunlight and nearly still air may be 10 to 20 °C warmer than ambient air, approaching its upper limit of 55 to 60 °C (e.g. Gates, Tibbals & Kreith, 1965; Loomis, 1965), this adaptation may be primarily for increased heat dissipation (reduced BL thickness) by lobes, and perhaps increased thermal conduction to outer edges due to the increased thickness. Eliminating radiation and transpiration effects on leaves of white oak (*Quercus alba*), Vogel (1968) found consistent 20% reductions in the leaf-air temperature differences for sun leaves relative to shade leaves.

(*a*) *Lobes and serration.* Lobes and serration reduce effective leaf dimension, reducing average BL thickness (and BL resistance) compared with a leaf with equal surface area but smooth margins (Baker & Myhre, 1969; Gottschlich & Smith, 1982). Givnish (1979) (as cited by Gottschlich & Smith, 1982) hypothesized that serration may also have evolved as an adaptive modification to reduce plant material between leaf veins, which is less supplied with water during water stress conditions.

Shape factors are most important at low wind-speeds where BL resistance is no longer small compared with stomatal resistance. Gates (1962) already showed that re-radiation is inadequate to prevent lethal temperatures in leaves, leaving evaporative and convective cooling as control mechanisms. The heat transfer simulations of Vogel (1970), with models of highly lobed sun leaves and modestly lobed shade leaves of white oak, and various indented or star-shaped disks with circular symmetry, demonstrated the importance of leaf shape on orientation effects in free convection. As mentioned in section VII.2, orientation from horizontal to vertical position caused small change in overall transfer for the irregular, deeply serrated shapes. Thus, a leaf orienting itself vertically will significantly improve its convective heat dissipation ability only if it is unlobed. Perhaps not coincidentally, unlobed leaves of blackjack oak (*Quercus marilandica* Muench.) in the Carolina Piedmont have practically no leaves in the horizontal plane (Vogel, 1970). Not surprisingly, temperature gradients were greater near the leaf margins of lobed models, to a degree that depended on the irregularity of shape. This suggests a functional significance of structural features (including insect-eaten holes) in horizontal leaves that permit buoyancy-driven flow across, rather than around the leaf. Flow-through reduces the self-insulating effect on the leaf from the envelope of 'preheated' BL fluid streaming off the lower (upstream) side in free convection from a leaf warmer than ambient air.

In forced convection Vogel (1970) found little difference in heat dissipation per unit area between sun and shade leaf models in parallel flow, but in inclined flow the more irregular sun leaf dissipated heat more effectively (23% *vs.* 14% enhancement over the circular plate), and the increase in transfer with increasing velocity was more consistent for irregular shapes than circular plates. Effects of serration near the leading edge increased transfer on square plates by up to factors of 1·4 at low angles of attack, broadening the range of angles Θ over which significant transfer enhancement is observed (Chen *et al.*, 1988*b*; section V.2*a*).

Serration may well serve more than one purpose, including perhaps a deterrent effect on herbivores, but increase in heat dissipation through reduction of BL thickness and a lessening of orientation effects appear to be primary effects. Leaf tearing for large leaves such as banana (*Musaceae*) in high-temperature environments may be seen as a related example of this protective mechanism against lethal temperatures (Taylor & Sexton, 1972, as cited by Grace *et al.*, 1980).

(*d*) *Raschke's question revisited.* We may now revisit the question addressed by Raschke (1956) and his contemporaries (section II), whether an increase in BL thickness will lead to increased or decreased transpiration. Increased BL thickness (resistance) will tend to reduce convective heat and moisture loss and lead, through reduced heat loss, to higher surface temperature. Since vapour pressure is exponentially dependent on temperature, this effect would tend to increase transpiration, counteracting the effect of increasing BL thickness to a degree that depends on the relative magnitudes of BL and stomatal resistances and plant physiological response. The question does not have a general answer, therefore, but specific answers are increasingly sought through numerical simulations integrating physical and physiological aspects of leaf modelling, such as the simulation of gas and energy exchange of a leaf of a C-3 plant by Collatz *et al.* (1991). Their stomatal model considers the (variable) leaf BL both as a local environment for the stomata and as a physical boundary, separating physiological processes within the leaf from the transport processes between the leaf and ambient air. It differs from earlier models (e.g. Jarvis & McNaughton, 1986) in treating the stomatal conductance g_s not merely as a more or less constant factor which determines the lower boundary conditions for BL transfer processes, by including feedback mechanisms between the BL and the (variable) value of g_s. (For further discussion see section IX.4.)

(*e*) *Photosynthesis and water use efficiency*. The effect of leaf shape on crop productivity or water use efficiency (WUE) also must consider BL thickness in its interaction with canopy structure (penetration of radiation and wind), and feedback through stomatal response (Zangerl, 1978). It is difficult to describe these interactions explicitly in models (section IX.4), or to generalize field observations, because of the many simultaneously interacting parameters and species-specific feedback. Baldocchi *et al.* (1985), in comparing two isolines of soybean (*Glycine max* L. Merill, ev. Clark) differing only in leaf width, noted increase in net radiation, temperature and sensible heat transfer, and decreases in humidity and vapour transfer in the looser, narrow-leaf canopy (NLC). On a leaf area basis, photosynthesis (CO_2 exchange) was enhanced for the NLC, but no significant difference was observed on a ground area basis. WUE, in terms of flux ratio of CO_2 to H_2O, was higher for the NLC. Model experiments suggest that in warm environments with low absorbed radiation, large leaves with thick BLs would have an advantage in WUE through reduced transpiration (Parkhurst & Loucks, 1972). This agrees qualitatively with estimates of Geller & Smith (1982), who observed and simulated reduced transpiration (by up to 20% for a full day) for the larger leaves of *Frasera speciosa*, *Balsamorhiza sagittata* and *Rumex densiflorus*. However, due to the non-linear dependence of BL thickness on leaf size (section I), size-related effects are only significant for small leaves, where BL thicknesses are most sensitive to leaf size variation. Doubling the leaf size from 20 cm to 70 cm, for example, would reduce daily transpiration by a mere 2 to 5% according to the model simulations of Geller & Smith (1982).

When analyzing effects of leaf shape on transfer, we must realize that shape-related differences in BL thickness, clearly demonstrated in wind tunnel experiments, do not necessarily translate into a commensurate advantage in photosynthesis in the field (Baker & Myhre, 1969). This is most likely attributable to effects of leaf orientation, with associated changes in radiation interception (shading), which may override the effect of BL thickness (Geller & Smith, 1982; Smith, Schoettle & Cui, 1991).

2. *Fine structure of leaf surfaces*

(*a*) *Pubescence*. Leaf hairs occur in a variety of structures and densities. They may have adaptive significance, potentially affecting leaf energy and gas exchange through changes in BL thickness and radiative properties, preventing stomatal obstruction and perhaps providing protection from herbivores (Gates, 1980). It is not possible to generalize the effect of leaf pubescence on BL thickness: widely spaced hairs may enhance mixing near the surface, reducing aerodynamic resistance, while a dense hair cover will add a stagnant air layer trapped between poorly conducting hairs, increasing effective BL thickness. Dense pubescence thus partially decouples BL thickness from fluctuations in wind speed, which strongly affect the BL resistance on hairless leaves (Meinzer & Goldstein, 1985). Most hairs on mature leaves consist of dead cells that would not provide the movement of water or protoplasma necessary for them to act as conductive 'fins' for augmentation of heat loss, as hypothesized by Wolpert (1962).

Since the physical model simulations of Wiegand (1910), leaf hairs have generally been expected to reduce transpiration in moving air through increased BL thickness, either significantly (Woolley, 1964) or negligibly (Ehleringer & Mooney, 1978). For example, observations on *Verbascum thapsus* leaves in a low speed wind tunnel (Wuenscher, 1970) showed warmer surface temperatures, essentially unchanged transmission and reflection of radiation, and reduced heat and moisture transfer for the natural, pubescent leaf against shaved leaves. The reduction of energy fluxes was compensated by an increase in emitted thermal radiation due to the increased surface temperature. Wuenscher's use of a BL resistance of $\approx 2d/3\alpha$ (where d and α are thickness of hair cover and thermal diffusivity of air, respectively) implies the existence of a stagnant air layer of effective thickness $2d/3$. Such observations may be typical only for the given leaf morphology and physiology, at the given low levels of free stream turbulence, which may have exaggerated the insulating effect of the hair cover. As a consequence, caution must be exercised when generalizing observations, and apparently contradictory results may well be observed (as reviewed e.g. by Wuenscher, 1970).

Combining field and laboratory observations with numerical simulations, Meinzer & Goldstein (1985) also showed increased leaf temperature in thick leaf pubescence (hairs up to 3 mm), on the Andean giant rosette plant *Espeletia timotensis*, under conditions of high incident solar radiation. Pubescent leaves, more decoupled from ambient wind speed, were more directly coupled to incident solar radiation and able to maintain a higher surface temperature. The effect was most pronounced at low ambient temperatures Ta. Expressing the effect of pubescence through a BL resistance d/α, i.e. assuming an effective stagnant air layer with thickness given by the thickness of the pubescent coat, their results represent an upper limit for expected effects. For example, at $Ta = 5$ °C and wind speed of 2 m/s, surface temperature with 2 mm pubescence was 16 °C, compared with 10 °C for the non-pubescent leaf of the same size. At $Ta = 20$ °C, the difference decreased from 6 to 3°. For transpiration, the effect depended on the relative magnitude of BL resistance to stomatal resistance, and could result in a small increase or even a decrease in transpiration in spite of the elevated surface temperature.

In general, there is some consensus expectation of reduced transpiration as a function of pubescence, but little agreement on expected effects on photosynthesis. Effects of increased aerodynamic resistance would be expected to be relatively less significant, compared with the corresponding effect on transpiration or heat transfer, because of the larger mesophyll resistance to CO_2 exchange. Baldocchi *et al.* (1983) measured fluxes of heat, moisture and CO_2 above canopies of *Glycine max* L. Merr. cv. Harosy, two soybean isolines differing by a factor of four in density of leaf pubescence. No systematic difference was observed in net radiation and CO_2 flux, while transpiration was reduced from 300 to 276 W m^{-2} and sensible heat flux increased from 74 to 100 W m^{-2} for the more pubescent isoline. Thus, energy partitioning was altered, as well as water-use-efficiency, which became more favourable (3·89 *vs.* 3 mg(CO_2) g(H_2O)$^{-1}$. Interestingly, no systematic difference was found in stomatal resistance, suggesting that these changes are primarily BL effects. Interpretation of such results must also consider the possibility of altered spectral properties of the leaves, which could result in changes in radiation penetration into the canopy.

(*b*) *Stomatal distribution.* The interaction between BL characteristics and stomatal distribution on the leaf surface has not yet been studied extensively. The model simulations of Foster & Smith (1986) demonstrated the complex interaction between stomatal distribution patterns and transfer from horizontal leaves in the transition region from forced to free convection. Maximum effect is found for sunlit leaves with high stomatal conductance, at wind speeds $< 0{\cdot}5$ m s^{-1}. Not surprisingly, hyperstomatous leaves had higher transpiration than hypostomatous ones when free convection effects started to become dominant, to a degree that depended on leaf size and stomatal response. For leaves with low stomatal conductance, stomatal distribution had little effect. Non-uniform stomatal closure as a response to stress could conceivably lead to significant error in estimates of stomatal resistance based on observation of vapour transfer in situations such as leaf chambers, where the leaf BL resistance to vapour transfer is presumed to be known (Van Kraalingen, 1990). Van Kraalingen's error estimates made the unrealistic assumption that stomata are either fully open or fully closed. Recent models of leaf-level photosynthesis (Cheeseman, 1991) permit more subtle distributions of heterogeneous stomatal conductance but have yet to reproduce satisfactory photosynthetic characteristics. The interactions between patchy stomatal closure and the potentially very heterogeneous (and time-varying) distribution of BL thickness, as seen indirectly in the spatially varying pattern of leaf surface temperature in Figure 1*b*, are not addressed in current models.

3. *Adaptive significance*

Speculations on the evolution of leaf morphology as an adaptive response to local microclimate are not new (Bailey & Sinnot, 1916). Caution is advised when using parameters relating to leaf shape and hairiness as taxonomic keys in some plant species, because their 'phenotype plasticity' permits them to adapt to environmental stimulus (Menadue & Crowden, 1990). Geller & Smith (1982) presented an overview on the question of leaf size and orientation. Large leaves generally tend to be more sensitive to changes in the amount of absorbed radiation because their thicker BLs potentially permit them to reach larger leaf-air temperatures differences, while smaller leaves are more directly coupled to ambient air (Gates, 1976). The tendency of large leaves to exhibit lowered transpiration and more favourable WUE, under appropriate microclimate conditions, has already been mentioned (section VIII.1*e*). As pointed out by Geller & Smith (1982), evolutionary adaptation of leaf size to transpiration constraints (if such is indeed the case) might be aiming at response to critical periods in daily or seasonal cycles, rather than daily peak or average transpiration.

The potentially adaptive function of leaf pubescence to conserve water – as opposed to a waxy or resinous coating – was already discussed by Weigand (1910). He speculated that pubescence, which is more effective at high wind speeds, may have evolved as an attempt to reduce peak demands while maintaining efficient stomatal exchange at low wind speed. The question is explored by Meinzer & Goldstein (1985) through the example of the high-elevation Andean giant rosette *Espeletia timotensis*, under conditions of high incident solar radiation and low environment temperature. Since the increased BL thickness from a coating of hair partially decouples the leaf surface (and its temperature) from ambient wind, its primary effect in cooler climates would be an increase in surface temperature, with very minor alteration of the radiation balance. The simulations of Meinzer & Goldstein (1985), supplemented by field observations, indicated that pubescent leaves in a cool environment might enjoy a temperature advantage of the order of 7°, with small corresponding increase in transpiration (17%). By contrast, a similar increase in the surface temperature of non-pubescent leaves would result in a doubling of the transpiration rate in their numerical simulations. Such differences point to a selective advantage at high elevations with high radiation levels and suboptimal ambient air temperatures; the higher temperatures favour assimilate translocation and leaf growth, while water is conserved without stomatal closure that would reduce photosynthesis. A similar effect could, in principle, be achieved by increasing leaf size but, as discussed in section VIII.1*e*, such an increase would have to be substantial and fluctuations in wind speed would make this mechanisms ineffective. Such high-altitude adaptations resemble the adaptation of desert plants in so far as both could be interpreted as an attempt to shield the plant against unfavourable ambient temperatures.

In all such discussions we must keep in mind that it would be unwise to expect simple physical arguments to provide a satisfactory interpretive framework for morphological adaptation. The large number of physical parameters of shape, surface structure (including pubescence) and mechanical, anatomical or physiological characteristics that could be modified to optimize photosynthesis, water use and temperature regimes, or adapted to adverse aspects of nutrient availability, microclimate and perhaps herbivore pressure, may well preclude readily apparent cause–effect relationships (Parkhurst & Loucks, 1972; Rausher, 1978; Smith & Geller, 1980; Ashton & Berlyn, 1992). This makes apparently contradictory observations inevitable. At a minimum, 'phenotype plasticity' is seen as a 'buffer, enabling a species to occupy a range of habitats' (Menadue & Crowden, 1990).

4. *Boundary layer microclimatology*

(*a*) *Leaf wetness*. The presence of liquid water on the leaf surface is a determining factor for the terrestrial energy balance (through partitioning of incoming energy into transfer of sensible heat and moisture), for the development of pathogens in fungal diseases which usually require a period of leaf wetness to complete a cycle of infection (Van der Wal, 1978), for dry deposition of atmospheric pollutants (Schuepp, 1989; Unsworth & Wilshaw, 1989; Wesley, Sisterson & Jastrow, 1990), for the deposition of ozone to vegetation (Fuentes *et al.*, 1992), or for the ability of leaves to neutralize acid rain (Adams & Hutchinson, 1987). Of particular interest is the duration of leaf wetness, which is a function of BL moisture transfer (see e.g. Huber, 1992, for a recent review).

Predictions of evaporation from canopies and leaf wetness duration often use a 'combination equation' (such as the Penman–Monteith P–M expression (15) in section IX.2, with vanishing stomatal resistance). The Rutter model (Rutter *et al.*, 1971; Rutter, Morton & Robins, 1975; Rutter & Morton, 1977) is a popular example and formed the basis for many subsequent modifications. Early models typically made the assumption that all leaves are either wet or dry (Calder, 1977), while subsequent modifications incorporated 'wetted areas' into single- and multilevel developments (Sellers & Lockwood, 1981; Hancock, Sellers & Crowther, 1983). The multilayer resistance model of Thompson (1981), based on the P–M equation, used average leaf BL transfer approximately 25% above the Pohlhausen (7) prediction, which is not unreasonable on the basis of our review, considering enhancement through turbulence and shape factors, with coincident potential reduction through sheltering.

Wronski (1984) addressed the interesting question of whether leaves in the wet part of the canopy should be treated as if covered by a uniform water film (surface layer retention hypothesis) or by discrete water droplets (drop retention hypothesis). In the latter case, the BL resistance of individual droplets must be introduced, possibly with a shelter factor. The water repellency of leaves, which governs the relative partitioning between film and drop formation may have more importance than the paucity of studies suggests (Smith & McClean, 1989). The recent study of BL transfer from leaf water droplets (Butler, 1990) compared observations in the natural environment against electrochemical laboratory simulations under uniform temperature conditions (Leclerc, Schuepp & Thurtell, 1986). Expressing droplet transfer in the form of (8), Butler's mass transfer data could be described by $c_m \approx 0{\cdot}66$ and $n \approx 0{\cdot}4$, based on droplet diameter as characteristic length L. His predictions for drop evaporation rates were lower than those based on electrochemical simulations ($c_M \approx 0{\cdot}76$ and $n \approx 0{\cdot}47$), but the difference vanished when thermal conduction from the leaf into the drop was included in the estimate.

(*b*) *Dispersal of particles*. The dispersal of pollen or pathogens in canopies is of great biological and economic significance. Spores of many fungal pathogens are passively liberated by gusts of wind which temporarily disrupt the BL (Aylor, 1990). Early work on spore liberation from leaves by wind (Grace & Collins, 1976, and work cited therein) noted an apparent incompatibility between the wind speed required for spore liberation (several m s^{-1}) and the strongly attenuated wind speeds observed in leaf BLs (Fig. 1*a*). In steady-state BL simulations, hurricane-strength external winds would in fact be required to liberate a significant fraction of spores in a canopy (Grace & Collins, 1976). However, in-canopy wind regimes are characterized by approximately log-normally distributed gusts of up to five times the average wind speed (Shaw, Ward & Aylor, 1979; Shaw & McCartney, 1985). This, again, stresses the fact that the BL descriptions given above should be seen as time-averaged characteristics, with strong fluctuations often engendering non-linear response. The role of intermittent wind on dispersal of pathogens, and models used in its description, have been reviewed by Aylor (1990).

(*c*) *The BL as microhabitat*. Quite apart from their role as a buffer in heat and mass transfer between leaves and their environment, leaf BLs also represent a habitat for micro-organisms of biological or economical significance. Temperature and moisture are the determining factors of the microclimate, and dehydration the most likely threat. A review of leaf microorganisms is beyond the scope of this review, but the question is illustrated by example (Ferro & Southwick, 1984). The ($\leqslant 300\ \mu$m thick) spotted spider mite *Teranychus urticae* Koch, which causes extensive crop and orchard damage, exists with eggs and nymphs in the leaf BL. Ferro & Southwick examined the question of local humidity for the mite eggs (diam 150 μm) under the simplified assumption of a linear humidity profile across an assumed 3 mm BL, using observed leaf and ambient temperature data. For fully transpiring leaves at 26 °C, vapour density at the leaf surface would be close to the saturation value of 24·4 g m^{-3}, and the difference in vapour density across the BL would be 10 g m^{-3} for the assumed ambient temperature of 35 °C with relative humidity of 35 %. The local humidity at the distance of the egg (0·15 mm = 5 % of BL thickness) would therefore only be 0·5 g m^{-3} lower than the surface value of 24·4 g m^{-3}. This would lead to minimal mortality, since observations showed that extended exposure to airflow of 14 g m^{-3} is required for 50 % mortality (Ferro & Southwick 1984). Even a compressed BL (to 0·5 mm) would only lower the humidity at a distance of 0·15 mm to $\approx$ 21 g m^{-3}. An overview of microhabitats, including some information on leaf BLs, is given in Stoutjesdijk & Barkman (1992).

IX. LEAVES IN PLANT CANOPIES

1. *Plant-atmosphere coupling*

The problem of relating a plant to the spatially and temporally varying canopy environment has been the subject of comprehensive review (e.g. Monteith, 1981; Denmead, 1984; Jarvis & McNaughton, 1986; Finnigan & Raupach, 1987) and the focus of many recent studies as discussed below. It can be approached from the viewpoint of individual leaves (physiological approach), usually through a 'combination equation' that includes the leaf energy balance, all the way to the description of plant communities as a continuum, describable by mean quantities and fluctuations subject to conservation equations. Jarvis & McNaughton (1986) examined the different conclusions drawn by physiologists, who tend to examine single leaves or plants in laboratory situations with small aerodynamic resistance and predominantly stomatal control of transpiration, and meteorologists, who tend to see plants as passive wicks evaporating water according to available net radiative energy. The transpiration rate (λE_L) from a leaf with negligible BL resistance is essentially determined by stomatal conductance (g_s), such that $d(\lambda E_L)/(\lambda E_L) \approx dg_s/g_s$. A thick leaf BL will increasingly decouple the stomatal exchange from ambient conditions, lessening the relationship between changes in stomatal conductance and changes in the transpiration rate by a 'decoupling factor' Ω (Jarvis & McNaughton, 1986), defined by $d(\lambda E_L)/(\lambda E_L) = (1\text{-}\Omega)\ dg_s/g_s$. Values of Ω range from 0 to 1 and (as tabulated by Jarvis & McNaughton) might be 0·01 for spruce needles (coupled to ambient air flow through extremely thin BLs), and 0·97 for large, tropical leaves. While this concept ignores the complexities of feedback between stomatal and BL conductance (Collatz *et al.*, 1991, see below), it provides an introductory analogy to our understanding of plants within the canopy. Feedback on the canopy microclimate from the plants (leaves) will tend to decouple leaf energy and mass exchange in the canopy from conditions of temperature and moisture outside the canopy by a similarly defined parameter Ω (Jarvis & McNaughton, 1986). The latter in essence quantifies the effectiveness of aerodynamic coupling between plants and ambient airflow through a canopy BL. Aerodynamically smooth canopies, such as tea gardens, would be examples of highly decoupled systems. Updated modifications of decoupling factors specifically adapted to regional descriptions of plant-atmosphere exchange include sensitivity to changes in vegetation cover, radiative properties and stem/leaf area ratios (Pinty *et al.*, 1992). Specific attempts to deal with plants in more or less decoupled canopy stands are briefly summarized below, to the extent that they require explicit or implicit information about leaf BLs.

2. *The physiological approach*

In the Penman formulation, as modified by Monteith (1963, 1965), henceforth referred to as P–M, the transpiration of λE of a single leaf (subscript L) may be written as a combination equation

$$\lambda E_L = \frac{sR_L + \rho c_p \delta e / r_a}{s + \gamma\,[1 + (r_s/r_a)]}, \tag{15}$$

where R, ρc_p, δe, r_a and r_s are net radiation, volumetric heat capacity, ambient vapour pressure deficit, aerodynamic and stomatal resistance, respectively. s and γ are slope of the vapour-pressure *vs.* temperature curve and psychrometric constant, respectively. Provided that appropriate definitions are given for the locations relative to which the vapour pressure deficit is defined, and for the aerodynamic resistance r_a, (15) can also be adapted to describe transpiration from isolated plants or trees (e.g. Landsberg & McMurtrie, 1984) or plant canopies (see below).

When estimating canopy transfer on the basis of leaf transfer, the total leaf area and its subdivision into individual leaves of various shapes, sizes and BL properties, with their local radiation and wind environments, should be known in principle, at least in a statistical sense. Total leaf area is usually expressed through the leaf area index (LAI), traditionally defined as total one-sided leaf area per unit ground surface for broad leaves. Radiation interception is then given by projection in a plane perpendicular to incident rays, a procedure clear in principle for flat, broad leaves, but in need of re-examination for more complex foliage structures (Chen & Black, 1992).

In order to avoid the logistic problem of sampling and integrating a sufficient number of leaves for a representative canopy description, (15) is often applied to the canopy as if it were a single 'big leaf' located at the place of effective momentum absorption (Monteith, 1963; Sinclair, Murphy & Knoerr, 1976). Exchange is then seen as taking place between the 'leaf', and air at a reference level above the canopy, although the heights of absorption for momentum, heat and vapour are not identical (Thom, 1975), and distribution of leaf area and stomatal resistance r_s throughout the canopy are in fact required data. Leaf aerodynamic and stomatal resistances r_a and r_s in (15) are then replaced by the aerodynamic resistance of the canopy and an internal 'canopy resistance' r_c (see e.g. Monteith & Unsworth, 1990) which have to be determined more or less empirically.

The P–M approach is appropriate to situations where leaves can reasonably be described by one set of parameters, or stratified into layers where properties may be considered to be uniform (e.g. Shuttleworth, 1976; Jarvis, Edwards & Talbot, 1981; Lhomme, 1988). This approach has generally been successful in well ventilated canopies with small foliage elements (small BLs), where aerodynamic resistance is small compared to stomatal resistance (such as Tan, Black & Nnyamah, 1978). It is not a practical approach for mixed stands and irregular terrain, and it does not include stability (thermal buoyancy) effects. Other limitations, as discussed e.g. by Philip (1966) and Denmead (1984), concern the local variability in diffusion resistance between different leaves, leading to strong variations in energy partitioning due to the non-linearity of the P–M equation. The limitations of the P–M expression in partially wet canopies, where water does not either pass entirely through the stomata or evaporate from a completely wet canopy with vanishing stomatal resistance, have been briefly alluded to in section VIII.4*a* and will not be pursued here. Such reservations do not detract from the enormous contribution made to the understanding of leaf-atmosphere interactions through these early physiological models. They have become a classical tool and their limitations only serve to highlight the added degree of complexity introduced by consideration of leaves in the complex canopy environment. The tendency of physiological models to produce unrealistic stomatal feedback mechanisms (Choudhury & Monteith, 1986; Sellers *et al.*, 1986) are currently being corrected (Sellers *et al.*, 1992) as discussed below.

3. *The conservation equations*

As an alternative to the physiological approach, plant communities may be viewed as a physical continuum with random or non-random internal leaf distribution, subject to conservation equations of momentum, energy and mass (see e.g. the summary by Finnigan & Raupach, 1987). For reasons of transparency we will merely follow this approach qualitatively in a space-fixed (Eulerian) frame of reference, in so far as it touches on the question of leaf BLs and leaf transfer processes. The conservation equation for heat, for example, states that any input of energy into a given volume of canopy space, whether by radiation or thermal advection, must either be compensated by an equal energy outflow, or balanced by sources or sinks for energy within the volume. A similar argument must apply to the balance of moisture or CO_2. Since changes in heat and moisture storage within canopies are relatively small under most conditions, leaves are the dominant sources or sinks in canopy space. Specification of source and sink distributions for heat, vapour and CO_2 in the continuum equations, therefore, generally reduces to a need to specify leaf distributions and leaf-air exchange processes throughout the canopy. This task, which in principle implies the description of distributions of leaf area, morphology and orientation, the dynamic behaviour of leaves (fluttering) and their local environment, is clearly formidable for a model applicable to heterogeneous plant stands (Monteith, 1981). The spatial complexity of leaf distributions in canopies is usually dealt with through a process of volume averaging (Finnigan, 1985), with vertical temperature or concentration profiles in canopies related to horizontally-averaged source or sink distributions (Raupach, Denmead & Dunin, 1992). Likewise, factors such as contributions to turbulence from drag and motion (waving) of leaves are usually added to the control volume in a volume-averaged form.

Apart from the challenge associated with a realistic description of source and sink distribution, this approach suffers from the difficulty of describing the intermittent turbulent transport in and out of the control volume in the face of very irregular (and often dissimilar) distributions of sources and sinks for heat, moisture and CO_2, and the somewhat arbitrary assumptions (closure assumptions) that have to be made to produce a 'closed' system of equations, where the number of variables matches the number of equations.

4. *Integrated models*

Integrating our understanding of leaf transfer processes into a broader picture of plant–atmosphere interaction is part of a rapidly expanding field which transcends the scope of this review. However, a few main lines will be sketched, somewhat arbitrarily subdividing models according to their principal orientation.

Agriculturally-oriented models try to describe crop productivity through photosynthesis, as a part of weather-dependent leaf exchange processes within the canopy. They tend to use ambient meteorological variables, data on crop microclimate, plant and soil status, and submodels for exchange processes between the various components of the soil–plant–atmosphere system, to describe canopy microclimate and biomass accumulation (e.g. the CUPID plant environment model by Norman, 1982, the corn growth model by Stewart and Dwyer, 1986, or the whole-plant simulation model by McCree *et al.*, 1990). They may be used in a prognostic mode, or for diagnostic evaluation of stress response (McCree *et al.*, 1990). It may be said that these models 'scale up' our understanding of plant–atmosphere exchange at the leaf (or even stomatal) level, into a canopy picture over space and time scales that are relevant to regional exchange processes and seasonal cycles.

Climatologically oriented models, on the other hand, tend to start from consideration of the large-scale energy balance, as surface boundary condition for global circulation models (GCM), gradually 'scaling down' from continental scale or mesoscale to a link with those elements (individual plant and trees and their spatial distribution patterns) which ultimately are responsible for the transport processes at the earth's surface. Models of this type, such as the Simple Biosphere Model (SiB) of Sellers *et al.* (1986), expanded the physiological approach to include a more complete description of the soil-canopy-atmosphere continuum, with a goal to link the small-scale exchange processes to GCMs. They contain physical and physiological descriptions of vegetation, including leaf BL resistance and shelter factors. The tendency of physiological models (including SiB) to produce unrealistic stomatal feedback mechanisms that preclude equilibrium solutions under conditions of plant water stress (Choudhury & Monteith 1986; Sellers *et al.*, 1986) are currently being corrected (in SiB-2, Sellers *et al.*, 1992) on the basis of the study by Collatz *et al.* (1991). The latter modelled the leaf BL layer as a time-variable boundary between physiological processes within the leaf and ambient transport processes, with feedback mechanisms between BL transfer processes and stomatal conductance g_s (section VIII.1*d*). Predictions of g_s and photosynthesis showed good agreement with tests on intact natural soybean leaves, and predicted response patterns for transpiration through the course of an idealized summer day on the basis of a 'big leaf' assumption were encouraging. They include the mid-day depression of transpiration due to stomatal closure as a result of positive feedback mediated by the boundary layer, for high and low values of BL conductance which lead to excessive drying or excessive heating of the air at the leaf surface, respectively. Such simulations show a strong effect of BL conductance on leaf and canopy transpiration for otherwise unchanged environmental and physiological properties, with maximum transpiration at intermediate values of the BL conductance. Fig. 8 (reproduced from Collatz *et al.* 1991) illustrates the complicated modelled relationship between BL conductance *h* and stomatal conductance (*a*) or transpiration (*b*) during the course of a day. It suggests a previously unsuspected controlling importance of the leaf BL on regionally important exchange processes.

Parallel to these developments are attempts to couple models of plant–atmosphere exchange to the

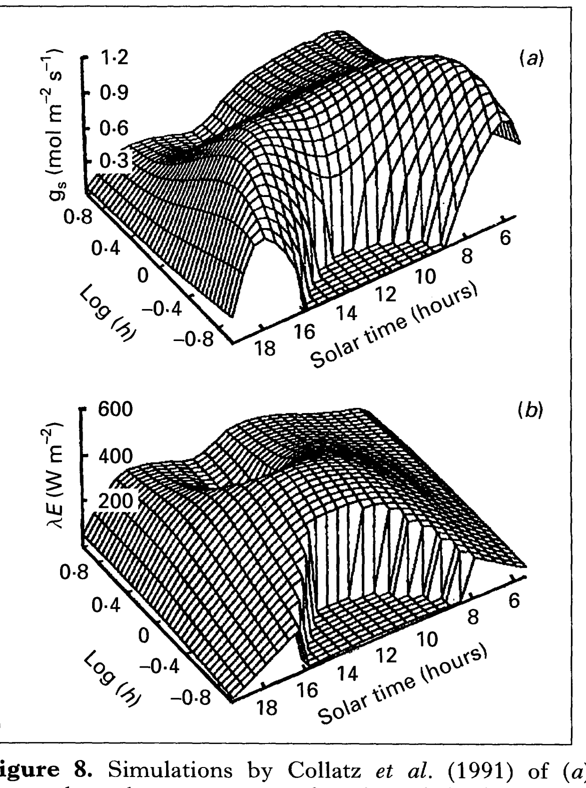

Figure 8. Simulations by Collatz *et al.* (1991) of (*a*) stomatal conductance g_s as a function of the log of BL conductance *h* and day time and (*b*) transpiration λE as a function of the log of BL conductance and day time. Conductances are given in mol m^{-2}s^{-1} which may be converted to m s^{-1} (used elsewhere in this review) by multiplying by 0·025.

convective boundary layer (e.g. Abdulmumin, Myrup & Hatfield, 1987; Raupach *et al.*, 1992). This interest has been sparked to a significant extent by a growing realization that exchange processes at the leaf level, particularly through their effect on energy partitioning, may affect mesoscale flow patterns in the planetary boundary layer (e.g. Avissar & Pielke, 1991). The modified model of Mascart *et al.* (1991), for example, studied the effect of vegetation on mesoscale motion through inputs on radiation and water stress terms (which determine stomatal resistance), with a suggestion that a shelter factor for leaves in the various canopy strata also be included.

The scope of leaf wetness studies may also expand in scale: Bass, Savdie & Gillespie (1991) established tentative links between synoptic weather patterns and expected statistics on frequency of occurrence and duration of leaf wetness periods and suggested that intergenerational development and large-scale dispersal of pathogen, geographical distribution of disease and long-term control strategies for plant disease, might benefit from integration of synoptic-scale considerations into leaf wetness modelling.

X. SYNOPSIS AND CONCLUSIONS

Attention to the leaf BL has fluctuated with the years. After some early pioneering studies, attention during the 1960s and 1970s focused on the formulation of dimensionless parameters, which expresses the dependence of leaf transfer processes for heat, moisture, CO_2 and (by analogy) gaseous pollutants on the molecular properties of the fluid and the characteristics of ambient wind (equations 7, 8 and 10). These descriptions, for free (natural) and forced convection, have been borrowed from engineering studies on standard geometric shapes such as flat rigid plates. Their applicability to realistic leaves in the natural environment demands largely empirical adjustments, dependent on leaf morphology (shape, roughness, pubescence), leaf motion, orientation against the flow, and free stream turbulence. With the exception of pubescence and aerodynamic sheltering, these factors tend to decrease BL thickness, increasing transfer effectiveness across the BL. Differences in observations of transfer across leaf BLs may often have been attributable to differences in the spectral characteristics of turbulence and its interaction with model geometry (e.g. aspect ratio). The dependence of leaf transfer processes on leaf size and morphology has naturally invited speculation as to their possible adaptive significance to environmental stimuli, whether as reversible phenotype 'plasticity' or genetically encoded as permanent adaptations.

To the extent that one can talk of consensus, the combined effects of leaf morphology, orientation, dynamic behaviour and wind characteristics on forced-convection transfer from isolated leaves is expected to result in a maximum enhancement by a factor of 2 over the value expected for equal-size smooth, flat plates in parallel flow. Enhancement by factors between 1·25 and 1·5 is a more likely expectation for randomly oriented, average leaves in natural canopy flow with small aerodynamic interference. Effects from various factors are not linearly cumulative, since perturbations imposed on an unperturbed BL will have a stronger relative effect than those superimposed on an already perturbed (compressed) BL. Similarly, mean transfer for randomly oriented leaves in free convection are likely to exceed those expected for smooth vertical plates by factors between 1·1 and 1·5, depending on surface roughness and absolute size, with enhancement increasing with decreasing size due to edge effects.

When integrating results of single-leaf studies into predictions of canopy response, aerodynamic interference between leaves and effects of leaf orientation and canopy structure on the radiation balance must be considered. In addition, the formulation of realistically variable leaf boundary layers in physiological plant models, with feedback on and through stomatal response, presents an ongoing challenge.

The coming years will see large, interdisciplinary field experiments in the areas of land surface climatology or trace gas exchange (e.g. tropospheric ozone and greenhouse gases). Intensive observations, taken locally, will not only have to be interpreted in the light of our understanding of all factors which affect the local measurement, down to the microscopic and microbiological level, but also extrapolated into regional predictions at scales accessible to remote sensing observations. Within this vast array of interlocking scales, the leaf BL is currently claiming its place as a modest but essential component of integrated models of surface–atmosphere exchange.

In addition, the leaf BL is also viewed increasingly as a microhabitat in its own right, amidst a growing awareness that many biological processes and organisms depend for their existence or survival on local deviations from average climatic parameters that may not be adequately expressed by spatially averaged climatic parameters.

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Appendix. *Table of symbols with SI units and common abbreviations*

AR	aspect ratio (ratio of alongwind length L to crosswind width W of leaf or leaf model [–]
BL	(leaf) boundary layer
c	concentration of mass in air (e.g. of water vapour or CO_2) [kg m^{-3}]
c_H,c_M	coefficient linking dimensionless expression for heat and mass transfer to dimensionless flow and fluid characteristics in forced convection (Eq. 8) [–]
D	molecular diffusivity of mass in air [$m^2 s^{-1}$]
e	vapour pressure of water [Pa]
F_H	heat flux density (heat exchanged per unit area per unit time) [W m^{-2}]
F_V	water vapour flux density [kg m^{-2} s^{-1}]
g_s	stomatal conductance [mol m^{-2} s^{-1}]
Gr	Grashof number (dimensionless number characterizing free convection owing to buoyancy around a leaf–Eq. 5) [–]
h	($= h_H$) heat transfer coefficient [J m^{-2} s^{-1} deg^{-1} = W m^{-2} deg^{-1}]; sometimes used to denote transfer in statements that are equally valid for heat and mass, such as in the definition of α in section V
h_T	h divided by the heat capacity (ρc_P) of air, giving it the same units as the mass transfer coefficient h_M [m s^{-1}]
h_M	mass transfer coefficient [m s^{-1}]
Hz	frequency (e.g. of wind fluctuations) [s^{-1}]
k	thermal conductivity of air [W m^{-1} deg^{-1}]
k_H, k_M	coefficient linking dimensionless expression for heat and mass transfer to dimensionless flow and fluid characteristics in free convection (Eq. 10) [–]
L	dimension in the direction of air flow; in particular characteristic dimension of leaf or leaf model as defined in section III.4 [m]
L_U	integral scale of turbulence in the direction of air flow [m]
LAI	leaf area index [m^2 m^{-2}]
m	exponent of Pr and Sc in Eq. (10) [–]
n	exponent of Re (Eq. 8) and Gr (Eq. 10), characterizing the dependence of transfer on velocity or buoyancy, respectively [–]; eddy shedding frequency in the Strouhal number S (in section V.1).
Nu	Nusselt number (dimensionless heat transfer coefficient–Eq. 3) [–]
p_d, p_s	shelter factors for reduction of drag forces of scalars (heat and mass) by mutual aerodynamic interference of leaves [–]
Pr	Prandtl number (ratio of kinematic viscosity to thermal diffusivity of air – Eq. 5) [–]
R	net radiation [W m^{-2}]
Re	Reynolds number (dimensionless number characterizing the dynamics of forced convection around a leaf – Eq. 5) [–]
s	slope of vapour-pressure vs. temperature curve [Pa $°K^{-1}$]
Sc	Schmidt number (ratio of kinematic viscosity to molecular diffusivity of mass in air – Eq. 5) [–]
r_a	aerodynamic BL resistance ($h_T{}^{-1}$ or $h_m{}^{-1}$) [s m^{-1}]
r_s	stomatal resistance [s m^{-1}]
Sh	Sherwood number (dimensionless mass transfer coefficient – Eq, 4) [–]
TI	turbulence intensity (square root of velocity variance divided by mean velocity) [–]
u, u'	mean value and fluctation of wind speed [m s^{-1}]
W	width of leaf in the direction perpendicular to air flow [–]
x	downwind distance from the leading ege of a leaf [m]
X	length of leaf segment in the direction of air flow [m]
α	thermal diffusivity of air [m^2 s^{-1}] in the definition of dimensionless transfer numbers (section 3.1); ratio of transfer coefficients of inclined to parallel flow [–] in sections V and VI
β	constant multiplier to express effect of turbulence on dimensionless heat or mass transfer of leaves [–]
δ	thickness of the aerodynamic leaf boundary layer [m]
δe	vapour pressure deficit [Pa]

Δ	difference between variables observed at two locations
ϵ	ratio of molecular mass of water to air ($\approx 0{\cdot}62$) [–]
γ	psychometric constant (Eq. 2) [Pa °K^{-1}]
λ	latent heat of evaporation of water [J kg^{-3}]
λE	latent heat flux (energy flux associated with evaporation of water) [W m^{-2}]
ν	kinematic viscosity of air [$1{\cdot}5 \times 10^{-5}$ m^2 s^{-1}]
ρc_p	heat capacity of air [J m^{-3} deg^{-1}]
σ	folilage density (as defined in shelter factors, section VI.3) [–]
Θ	angle of attack of wind on leaf or leaf model [degree or radians]

Subscripts H, M, T, V stand for heat, mass, temperature and (water) vapour. The subscript x indicates local values of a parameter at downwind position x on a leaf or leaf model.