

reception and offered the use of the Upper Library of the Old College for the Symposium Dinner. The Department of Forestry and Natural Resources of the University of Edinburgh hosted the poster session and provided refreshments. We are grateful to the staff of the Institute of Terrestrial Ecology at Bush, the Northern Research Station of the Forestry Commission and the Royal Botanic Gardens for accommodating our excursions. We would like to thank our staunch friends who gave up their time to help in the task of organising the Symposium, our secretaries who assisted us in our correspondence with the contributors and finally the staff of the Edinburgh office of Blackwell Scientific Publications with whom it has been a pleasure to work.

1. COUPLING OF PLANTS TO THE ATMOSPHERE

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ECOLOGY AND THE ATMOSPHERE

The theme of plants and their atmospheric environment is particularly appropriate for the last British Ecological Society symposium of the seventies—a decade in which this major aspect of physical ecology has made substantial progress. If, thirty years ago, the Society had tried to hold a meeting exclusively concerned with such a topic, the input from physics and meteorology would have been slender, perhaps confined to controversy about a new evaporation formula developed by a worker from Rothamsted. Following a similar theme, many microclimatic papers published in the fifties dealt with heat balance of vegetation and its relation to evaporation. In the early sixties, the International Biological Programme fostered closer collaboration between ecologists and microclimatologists and by the end of that decade, an IBP symposium at Trebon (Šetlík 1970) reviewed the related topics of light, carbon dioxide exchange and photosynthesis. Atmospheric ecology continued to develop and expand in the 1970s. The volume of work on pollution has grown rapidly; the subject of wind has achieved text-book status, and vapour pressure deficit has emerged from relative obscurity as a significant element in the microclimate of plants. All these topics are discussed in later chapters of this volume.

By 1979, the common ground between ecologists, physiologists and physicists has extended to the point where it is possible to begin a symposium by talking about how plants are 'coupled' to their environment using a physical concept in a biological context. Fig. 1.1 summarizes the nature of this coupling on several related scales. Continentally, the location of major biomes is determined by the general circulation of the atmosphere and, in particular, by the spatial and temporal distribution of rainfall, temperature and solar radiation. There is an element of feedback in the system because air masses become cooler and moister when they pass over extensive areas of transpiring vegetation. This aspect of cooling is difficult to quantify but meteorologists working on general circulation models have begun to

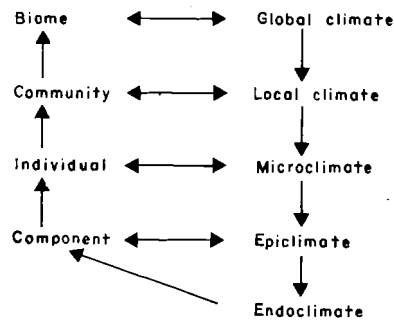


FIG. 1.1. The coupling of vegetation to the atmosphere: scales and interactions.

recognize the importance of specifying the physical behaviour of vegetation in an appropriate way.

Within the large scale global climate, local climates (sometimes referred to as meso- or topo-climates) determine the survival and rate of growth of plant communities and associations. The interaction of these communities with the climate imposed on them produces a microclimate to which individual members of the community are exposed. In a similar way, the interaction of the individual with its microclimate establishes a climate on an even smaller scale confined to the layer of air in immediate contact with components such as leaves, stems and inflorescences. Some workers refer to this as the teleoclimate (Gates 1968) but the Greek *τελος* means 'end' in a philosophical rather than a physical sense and a more appropriate term would be epiclimate from *επι* 'upon' or 'resting on'. Finally, the nature of the epiclimate determines the temperature of internal tissue, the gas concentration of inter-cellular spaces etc and these conditions could be called the endoclimate from *ενδον* 'within'.

It is the endoclimate which determines rates of growth and development of individual organs, thus establishing another system of feedback from the individual plant through the behaviour of communities to the biome.

This chapter is mainly concerned with the nature of epiclimates and with the coupling between plants and the atmosphere which occurs across the boundary layer of individual organs, a system which Grace describes in greater detail in the following chapter. Most attention will be given to the thermal characteristics of the epiclimate, partly because they illustrate a number of general principles and partly because several later chapters are concerned with the response of plants to temperature. The chapter by Unsworth deals with some aspects of the relation between epiclimate and microclimate.

THE CONCEPT OF COUPLING

Two systems are said to be coupled when they are capable of exchanging force, momentum, energy or mass. In physics, one of the most versatile forms of coupling is the electrical circuit in which energy in the form of charge moves from high 'potential' at a rate described as a 'current' (i). The simplest component of an electrical circuit is a resistor through which a current will flow when a difference of potential δV is maintained across it, and the 'resistance' of a resistor is defined as the potential difference needed to sustain unit current or $\delta V/i$.

The concept of resistance was implicit in the work of Brown & Escombe (1900) who measured the diffusion of water vapour and carbon dioxide in simple physical systems, relating their analysis to the processes of transpiration and assimilation by leaves. Maskell (1928) clearly identified the chain of resistances which govern the diffusion of CO_2 into a leaf. These early studies on single leaves were extended theoretically by Penman & Schofield (1951) and experimentally by Gaastra (1959). Comparable electrical analogues were then applied to the gas exchange of uniform stands of plants (Monteith 1963) and applications both to plant and to animal ecology are reviewed in several recent texts (Monteith 1975; Gates & Schmerl 1975; Campbell 1977). The flow of water through plants has also been analysed in terms of the drop in potential across a chain of resistances and according to Richter (1973), this line of work was initiated by Huber.

In analogues of heat and mass transfer, the potential of any entity Z is usually expressed as the amount of Z per unit volume of air and the rate of transport of Z is the amount moving through unit area of a system in unit time. Resistance then has the dimensions of time per unit length. The fact that these dimensions are independent of the nature of the entity is one of the main reasons for preferring resistances (or their reciprocals—conductances) to transfer coefficients of the type used by physicists and engineers.

The coupling of an organ to its environment can be described by a set of analogous electrical circuits, each describing the transport of a specific entity. There is no absolute scale of coupling; but if the resistance between A and B in a circuit is much smaller than the resistance between B and C , then A and B are said to be 'tightly coupled', and the comparison with B/C is implicit. A well known physiological example is the dependence of evaporation on stomatal resistance, r_s , and boundary layer resistance, r . Bange (1953) showed that when r_s is much larger than r , evaporation is almost independent of windspeed implying that the vapour pressure at the leaf surface is tightly coupled to the vapour pressure in the surrounding air.

The resistance analogues which have been widely used in physiology and ecology are appropriate for systems in a steady state, whereas the environment

of most organisms is continuously changing. Records of temperature, vapour pressure and wind near the ground reveal a complex spectrum of erratic fluctuations associated with turbulent eddies whose higher frequencies extend beyond 10 Hz. At the low-frequency end of the spectrum, random fluctuations with periods of several minutes merge into the systematic 24 hour cycle imposed by solar radiation. To explore the significance of these fluctuations in physical ecology, the concept of coupling can be extended to include components such as capacitances and inductances which determine the distribution of current through a circuit in response to changes of potential. The concept of capacitance has a number of applications in physical ecology including thermal problems discussed later. Inductance will not be considered further here because its relevance is more limited.

A capacitor (or condenser) is a device for accumulating and storing charge. When current i flows into a capacitor whose capacitance is C , the voltage across the capacitor increases at a rate which is proportional to the current and inversely proportional to C , i.e. $\partial V/\partial t = i/C$ so that $V = \int idt/C$. As the capacitor accumulates charge, V increases, opposing the flow of current which decreases and tends to zero when V is equal and opposite to the voltage in the rest of the circuit.

BOUNDARY LAYER RESISTANCE

Principles

In the steady state, the coupling of a plant organ to air passing over it depends on the resistance of its boundary layer, the epilimnate within which air movement is slowed by friction. Depending on the nature of the air-stream and of the surface, flow in the boundary layer may be either laminar, i.e. following smooth streamlines, or turbulent. Moreover, the pattern of flow can be determined either by an external pressure gradient—forced convection—or by a gradient of density established by a difference of temperature or of vapour pressure between the surface and the surrounding air—free convection. In plant ecology, rates of heat and mass transfer are rarely determined by free convection alone but in a very light wind, and especially over large leaves, forced and free convection may act together. Because hybrid convection is difficult to analyse, nearly all experimental work on heat loss from plant organs has been concerned with forced convection.

The depth of a boundary layer and the pattern of flow within it can be investigated with a hot-wire anemometer (Grace & Wilson 1976). The thermal boundary has been studied by Schlieren photography (Gates & Benedict 1963; Yabuki, Ishibashi & Miyagawa 1970); and the water vapour boundary layer with a microwave refractometer (Gates, Vetter & Thompson 1963).

It is characteristic of forced convection from smooth surfaces that the thickness of the boundary layer increases with distance from the leading edge and leaves exhibit this type of epilimnate when they are held rigid in a wind tunnel (see p. 35). The mean depth of the boundary layer depends primarily on air velocity and on the size and geometry of the object. Because the mean depth is usually two orders of magnitude less than the characteristic dimension of the object, the diffusion of heat, mass or momentum from a surface into the surrounding air occurs across the boundary layer, i.e. at right angles to the surface, rather than in the direction of the flow. If i is a flux per unit area and δV is the corresponding mean difference of potential between the surface and the free stream, i.e. across the boundary layer, the effective mean depth of the layer l is defined by the relation $i = D \delta V/l$ where D is a molecular diffusion coefficient. By analogy with Ohm's law, the resistance of the layer is $r = l/D^*$. For a given object at a fixed windspeed, the depth l is weakly dependent on the diffusion coefficient, being approximately proportional to $D^{1/3}$ (Grace, this volume). The depth is therefore different for heat, mass and momentum. Relevant values of diffusion coefficients and relative resistances were given by Jarvis (1971) and Monteith (1975).

Because the appropriate boundary layer depth of an object is rarely known *a priori*, resistances for forced convection are usually derived from standard formulae for heat transfer from objects of simple geometry, as tabulated, for example, by Leyton (1975) and Monteith (1975). From such formulae, resistances can be expressed in the form

$$r = Bd^{1-n}u^{-n} \quad (1.1)$$

where u is windspeed. The quantity d is known as the 'characteristic dimension' of the object, e.g. the downwind length of a flat plate, the diameter of a sphere, or the diameter of a cylinder with its axis at right angles to the flow. Table 1.1 contains values of the constants B and n to give r in units of $s m^{-1}$ when d is in m and u in $m s^{-1}$. Fig. 1.2 shows how the resistances of plates and spheres decrease with windspeed in the range

TABLE 1.1. Constants of equation 1.1 for calculating the boundary layer resistance ($s m^{-1}$) for heat transfer from an object with a smooth isothermal surface at an arbitrary temperature of 20 °C.

	d	B	n
Flat plate (uniform width crosswind; resistance for two surfaces in parallel)	downwind length	151	0.5
Cylinder (length effectively infinite; axis at right angles to airflow)	diameter	248	0.6
Sphere	diameter	175	0.6

* This symbol, r , is equivalent to r_a used by other authors (e.g. Chapter 2).

0.1 to 10 m s⁻¹ and increase with characteristic dimension in the range 0.3 to 10 cm. Plates with $d \approx 3$ cm exposed to windspeeds between 0.5 and 5 m s⁻¹ have resistances in the range 40 to 12 s m⁻¹ corresponding to mean boundary layer thickness in the range 2 to 0.5 mm on both sides of the leaf.

The corresponding resistance for free convection is independent of windspeed and is usually expressed as a function of $d^n/(T_o - T_a)^p$ where T_o is the surface temperature, assumed uniform, and T_a is air temperature. For laminar flow, $n = p = 0.25$. However, when the flow induced by buoyancy is turbulent rather than laminar—and turbulence is an inherent

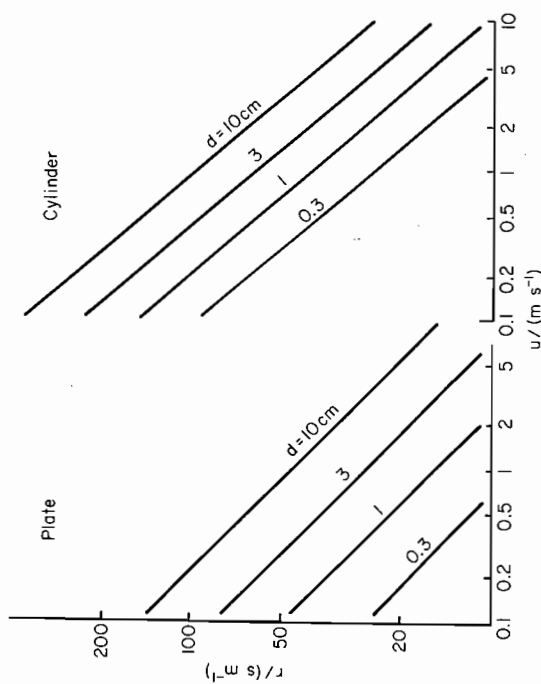


FIG. 1.2. Maximum value of boundary layer resistance for a flat plate (two surfaces in parallel) and a cylinder as function of windspeed u . The characteristic dimension d is the downwind length of the plate or the diameter of the cylinder and convection is forced.

feature of flow in plant communities even at low windspeeds—the index n is zero and $p = 0.33$. In units of s m⁻¹, the resistance for the upper side of a heated horizontal plate is then

$$r = 680/(T_o - T_a)^{1/3} \quad (1.2)$$

The relevance of equation 1.2 for vegetation has never been tested but in the absence of relevant field measurements, it can be used as a guide to the maximum value of resistance likely to be associated with a given value of $(T_o - T_a)$. When the resistance calculated for forced convection (eqn 1.1) exceeds the corresponding value for free convection (eqn 1.2), then eqn 1.2 should be adopted for further analysis. More exact criteria are discussed by Kreith (1973).

Ecologists are not concerned with the aerodynamic behaviour of smooth, flat rigid plates but with leaves with rough or hairy surfaces, often curved, and prone to flutter. Moreover, leaves (and stems) in plant communities are exposed to turbulent air in the wakes of their neighbours. How do these complications affect the coupling between plant organs and the microclimate of the canopy? The experimental evidence, some of which is contradictory, is briefly reviewed here in terms of boundary layer resistances and is discussed in terms of non-dimensional groups by Grace in the following chapter.

Several recent papers have been concerned with the extent to which the boundary layer resistance of an organ depends on turbulence in the airstream. In these studies, the effectiveness of turbulence is expressed as the ratio (β) of the resistance for a smooth, rigid object of simple and appropriate geometry (Table 1.1) to the smaller, measured resistance of the organ at the same velocity.

In wind-tunnel studies, turbulence has usually been induced in a somewhat arbitrary way by grids of wires or an array of obstacles. When windspeed is measured with a hot-wire anemometer in a circuit which records both instantaneous and mean velocities, u and \bar{u} , the intensity of turbulence (I) is defined as $\sqrt{(u - \bar{u})^2}/\bar{u}$. In plant communities, I often has a value in the range 0.4 to 0.7 (Legg & Monteith 1975), and it is not difficult to achieve this level in wind tunnels. However, the disturbance of a boundary layer by turbulence depends on the size of the eddies and not simply on their frequency as represented by an index of intensity. Transfer across the boundary layer is not affected either by very small or by very large eddies (Schlichting 1960) but by the spectrum of intermediate frequencies which deserve more attention in this type of study.

Haseba (1973a) attempted to generate turbulence with an appropriate spectrum by working in the airstream behind a canopy of citrus leaves. He estimated boundary layer conductances* ($1/r$) by measuring the rate of evaporation from a section of a model leaf. Fig. 1.3 shows the dependence of β on leaf area density (LAD) (cm²/cm³). For many agricultural crops, LAD is less than 0.1 so Fig. 1.3 implies that a figure of $\beta = 1.2$ should be representative of turbulence within a canopy. A similar result was obtained by Chamberlain (1974) who found $\beta \approx 1.25$ for the transfer of radioactive lead vapour to bean (*Vicia faba*) leaves and stems within a stand of plants on the floor of a wind-tunnel.

Nobel (1974a) found that the mean boundary layer depth of a wet cylinder, simulating a plant stem, decreased with increasing turbulence to

* In Japanese and Russian literature, conductances are often called transfer coefficients and given the symbol D .

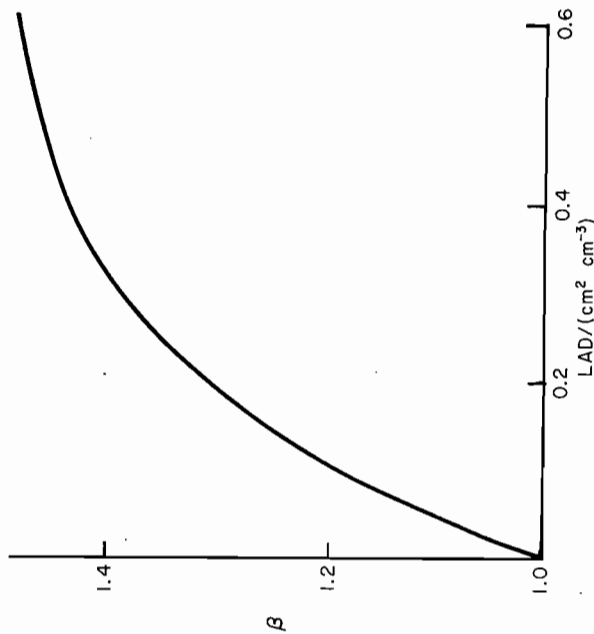


FIG. 1.3. Ratio of boundary layer resistance for isolated citrus leaf to resistance measured within a canopy of leaves of specified leaf area density (LAD); redrawn from Haseba (1973a).

give a maximum value of $\beta \approx 1.3$ when $I > 0.5$ (Fig. 1.4). In a similar study with wet spheres, simulating fruit or fungi (Nobel 1974b), β was about 1.16, consistent with the expectation that boundary layers surrounding completely streamlined objects should be more difficult to disturb by turbulence than those which are attached to flat plates.

Both Haseba and Nobel used rigid models and most of Chamberlain's measurements on bean leaves were made at windspeeds below the value of 2 m s^{-1} at which fluttering started. In experiments where model leaves have been forced to flutter at a frequency of 4 Hz, β reached a value of 2.7 (Parlange, Waggoner & Heichel 1971). However, when leaves flutter naturally in response to changes of windspeed and direction, β is likely to be substantially less than this figure.

Thorpe & Butler (1977) measured the resistance of the thermal boundary layer for leaves attached to apple trees growing in rows. For a set of measurements with considerable scatter, the mean relation between resistance and windspeed, measured between the rows, was close to the value predicted for a smooth flat plate, i.e. $\beta \approx 1$. By referring to measurements on the relation between windspeed and shelter (Landsberg & Powell 1973), Thorpe & Butler deduced that two effects were complementary: the decrease of windspeed between the alley and the canopy; and the increase of turbulence

within the canopy. Since the LAD was between 0.04 and 0.05 cm^{-3} , a value of $\beta = 1.1$ would be expected from Fig. 1.2.

Evidence in conflict with these figures was provided by Grace & Wilson (1976) who obtained $\beta = 2.5$ for a rigid metal plate simulating a poplar leaf. Furthermore, Wigley & Clark (1974), working with a model bean leaf in an airstream with $I \approx 0.35$, found that β increased from about 1.5 at 0.5 m s^{-1} to 3.0 at 4.5 m s^{-1} . Their evidence that β is a function of windspeed is not consistent with the more detailed work of Haseba (1973a).

Several workers have examined the dependence of resistance on the angle of inclination φ between a flat plate and the airstream. In general, the resistance of the windward side of a plate decreases as φ increases and according to measurements of evaporation by Haseba (1973b), β is about 1.2 for normal incidence ($\varphi = \pi/2$), irrespective of windspeed. The resistance of the leeward side increases with φ , and β is about 0.8 behind a plate when $\varphi = \pi/2$. Using radioactive vapour, Chamberlain was able to measure resistance as a function of φ and of distance from the leading edge. For a flat plate wetted on both sides, the resistance of the two surfaces combined in

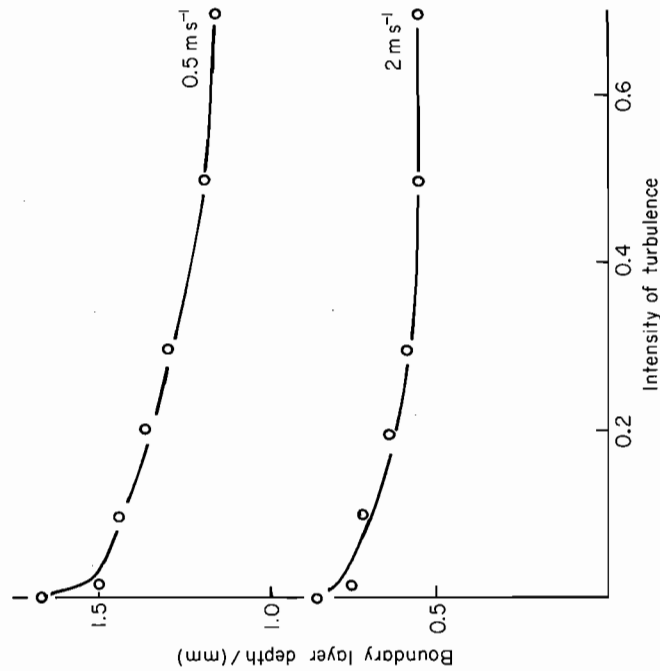


FIG. 1.4. Mean boundary depth for a cylinder of 10 cm diameter exposed in a wind-tunnel to specified windspeeds and turbulent intensities; redrawn from Nobel (1974a).

meter constant. For an amphistomatous leaf with a stomatal resistance of r_s for two sides in parallel ($2r_s$ on each epidermis), it is convenient to work with a modified psychrometer constant obtained by multiplying γ by the ratio of the total resistances for water vapour and for heat transfer, i.e. $\gamma^* = \gamma(r + r_s)/r$ (Monteith 1965). The corresponding formula for a leaf with stomata on one epidermis only is $\gamma^* = \gamma(r + 2r_s)/r$ and a more complex expression must be used if the two epidermises have different resistances.

For an amphistomatous leaf, the loss of latent heat is

$$\lambda E = \rho c [e_s(T_o) - e_a] / \gamma(r_s + r) = \rho c [e_s(T_o) - e_a] / \gamma^* r \quad (1.4)$$

where $e_s(T_o)$ is the saturation vapour pressure at leaf temperature and e_a is the value in the surrounding air. A form of expansion first used by Penman (1948) gives

$$\lambda E = \rho c \Delta(T_o - T_a) / (\gamma^* r) + \rho c \delta / (\gamma^* r) \quad (1.4a)$$

where Δ is the rate of change of $e_s(T)$ with temperature at a point between T_o and T_a and δ is the saturation deficit (i.e. $e_s(T_a) - e_a$). In practice, Δ is usually evaluated at temperature T_a . Neglecting metabolic exchanges of heat which are usually small and assuming for the time being that leaf temperature is constant, the sum of sensible and latent heat can be equated to the net absorption of radiant energy, i.e.

$$\mathbf{R}_n = \rho c (T_o - T_a) [1 + \Delta / \gamma^*] / r + \rho c \delta / (\gamma^* r) \quad (1.5)$$

For a non-transpiring leaf γ^* is infinite so that

$$\mathbf{R}_n = \rho c (T_o - T_a) / r \quad (1.5a)$$

Comparison of eqns 1.5 and 1.5a shows that the effect of transpiration on the heat balance of the leaf is twofold: the thermal resistance is reduced from r to $r' = r / (1 + \Delta / \gamma^*)$ and the heat load is reduced from \mathbf{R}_n to $\mathbf{R}_n - \rho c \delta / (\gamma^* r)$.

The value of an electrical resistance can be reduced from x to $x / (1 + \epsilon)$ by connecting a resistance x/ϵ in parallel. Eqn 1.5 can therefore be represented by the circuit shown in Fig. 1.5 with r and $r(\gamma^*/\Delta)$ in parallel, similar to the circuit described by Cowan (1972a). To make the role of stomatal resistance explicit, $r(\gamma^*/\Delta)$ is shown as the two resistors $r(\gamma/\Delta)$ and $r_s(\gamma/\Delta)$ in series. The net radiation is represented by a current generator. The opposing current $\rho c \delta / (\gamma^* r)$ can be introduced in two ways: as a battery of voltage $\rho c \delta / (\Delta + \gamma^*)$ in the main circuit; or more simply as a voltage $\rho c \delta / \Delta$ in series with $r(\gamma^*/\Delta)$. In the latter arrangement, the sensible heat fraction of the total current \mathbf{R}_n passes through r and the latent heat fraction through $r(\gamma^*/\Delta)$.

The potential across the pair of resistances is $\rho c (T_o - T_a)$. By evaluating the current flowing through the two branches of the circuit (or by manipulating

parallel was almost independent of φ . However, the difference in vapour resistance between windward and leeward surfaces would be significant for a leaf with stomata on one surface only.

The effect of leaf roughness on resistance has not been thoroughly studied, partly because of the problem of specifying or simulating the irregular surface of leaves. In related work on heat loss from rough cylinders, Achenbach (1974) showed that the main effect of increasing roughness was to lower the windspeed at which the boundary layer became turbulent—a point stressed by Grace (this volume) and Grace & Wilson (1976). Above this critical windspeed, there was a range in which resistance was proportional to u^{-1} rather than to $u^{-1/2}$ as in laminar flow.

In summary, it appears that the maximum resistance coupling a plant to its environment cannot exceed the value for a smooth flat surface. In the field, the effects of turbulence, fluttering, roughness and free convection combine to reduce the resistance by a factor $1/\beta$, usually between 0.5 and 1. The same processes combined with local differences of stomatal resistance make the distribution of temperature and other potentials far from uniform as Wigley & Clark demonstrated by thermography and this point is discussed later. At best, wind-tunnel measurements on real or model leaves are a useful guide to the way in which the foliage in a plant community is coupled to its microclimate. However, assuming that appropriate resistances for heat and mass transfer can be measured or estimated we now consider how they are used to calculate surface temperature and rates of transpiration.

SIMULTANEOUS HEAT AND WATER VAPOUR TRANSFER

When a leaf is transpiring, the extent to which it is coupled to the surrounding air depends on its stomatal resistance, r_s , as well as on the boundary layer resistances already considered. For convenience, and without significant loss of accuracy, the resistance to heat and vapour transfer by convection will be assumed to have the same value r . Different values can be used in the same analysis if required.

If we define the potential for sensible heat transfer as $\rho c T$, where ρ is the density and c the specific heat of air, the loss of sensible heat from a leaf with a mean surface temperature T_o to air at T_a is

$$C = \rho c (T_o - T_a) / r \quad (1.3)$$

where r is the boundary layer resistance for the two sides of a leaf coupled in parallel. The corresponding potential for latent heat transfer is $\rho c e / \gamma$ where e is vapour pressure (mbar) and γ ($= 0.66$ mbar K^{-1}) is the psychro-

eqn 1.5), the surface temperature can be expressed as the sum of air temperature and two terms which represent temperature differences, viz.

$$T_o = T_a + [rR_n/\rho c] - [\delta/(\Delta + \gamma^*)] \quad (1.6)$$

The first term in square brackets is an apparent increase in air temperature proportional to net radiation and for a non-transpiring leaf ($r' = r$) it is identical to the 'radiation increment' used by Burton & Edholm (1955) and other human physiologists. The second term in brackets is an apparent decrease in temperature proportional to saturation deficit.

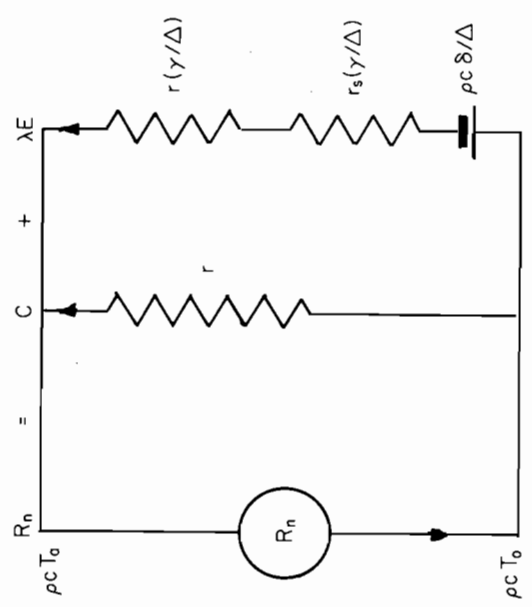


Fig. 1.5. Electrical circuit analogous to heat balance of transpiring leaf (eqn 1.5). The generated current R_n is partitioned between a current C passing through the resistor r and a current λE passing through a battery of voltage $\rho c \delta / \Delta$ and two resistors whose sum is $r_T \gamma^* / \Delta$.

The temperature T_o is the equilibrium mean surface temperature of an organ in a fixed microclimate (specified by R_n , δ , etc.). In a changing microclimate, T_o can be regarded as the effective temperature of the environment towards which surface temperature will move in an attempt to reach thermal equilibrium and in the next section, this quantity is given the symbol T_e .

Further analysis of the circuit gives the evaporation rate in the form

$$\lambda E = (\Delta R_n + \rho c \delta / r) / (\Delta + \gamma^*) \quad (1.7)$$

A full derivation is given by Jarvis (this volume).

Although equations 1.6 and 1.7 are formally exact, a minor modification is needed before they can be used to estimate the surface temperature and evaporation rate of a leaf in a specified microclimate particularly in problems

where r is treated as a variable. Then R_n must also be allowed to vary because it depends on the temperature of the surface over which the flux is measured, i.e. the term T_o is concealed in the right-hand side of equation 1.7. An appropriate procedure is to replace R_n by a fixed value of the 'isothermal' net radiation R_{ni} which is the net radiant flux the surface would absorb if it were at air temperature (Monteith 1975). The equation defining R_{ni} is therefore

$$R_{ni} = R_n + \sigma(T_o^4 - T_a^4) \quad (1.8)$$

where σ is the Stefan Boltzmann constant and the temperatures are now expressed in K. Because the difference between T_o and T_a is rarely more than a few degrees Kelvin, the term $\sigma(T_o^4 - T_a^4)$ can be replaced by $4\sigma T_a^3(T_o - T_a)$ with little error. This expression can be written in the same form as the corresponding term for heat transfer by convection if a radiative resistance r_R is defined by writing

$$4\sigma T_a^3(T_o - T_a) = \rho c(T_o - T_a) / r_R \quad (1.9)$$

from which

$$r_R = \rho c / 4\sigma T_a^3 \quad (= 213 \text{ s m}^{-1} \text{ at } 20^\circ \text{C})$$

Since convection and radiation are parallel modes of heat loss, the combined thermal resistance coupling a surface to its environment is

$$r_t = (r^{-1} + r_R^{-1})^{-1} \quad (1.10)$$

Retaining the convention that γ^* / γ is the ratio of resistances for water vapour and heat transfer (p. 11), γ^* is now defined as

$$\gamma^* = \gamma(r + r_s)(r^{-1} + r_R^{-1}) \quad (1.11)$$

where the first term in brackets is the total resistance to vapour transfer as before and the second term in brackets is the reciprocal of r_t . The corresponding value of r' to be used in eqn 1.6 is

$$r'_t = r_t / (1 + \Delta / \gamma^*) \quad (1.12)$$

with γ^* defined by eqn 1.11.

In his pioneering analysis of leaf heat balance, Raschke (1956) derived expressions for surface temperature and transpiration rate which are essentially the same as equations 1.6 and 1.7 but with an entirely different set of symbols and without reference to Penman's related work. The control of evaporation rate by stomata was expressed by a 'Wasserbedeckungsfaktor' proportional to $r/(r + r_s)$ in the nomenclature used here. It is therefore difficult to interpret graphs and tables in which r was treated as a variable whereas $r/(r + r_s)$ was assumed to have a constant value. This anomaly was corrected in a later paper (Raschke 1958) in which stomatal resistance was identified as a separate parameter and assigned appropriate values.

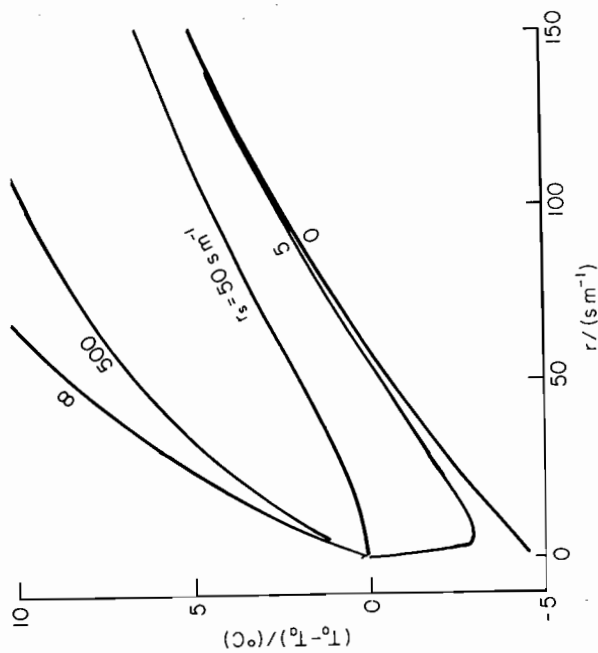


FIG. 1.6. Predicted difference between surface and air temperature for an amphistomous leaf in sunlight with specified boundary layer and stomatal resistances (for both laminae in parallel). Assumed microclimate: $R_{ni} = 300 \text{ W m}^{-2}$, $T_a = 20^\circ \text{C}$, $\delta = 10 \text{ mbar}$.

value, λE increases with decreasing windspeed and C decreases, implying that the curve for $T_o - T_a$ should be concave to the axis of r . When r_s is less than the critical value, the curve should be convex to the r axis.

The curves for $r_s = 500$ and 5 s m^{-1} demonstrate these differences. A value of $r_s = 500 \text{ s m}^{-1}$ is appropriate for a leaf with stomata partly closed by water stress, and $r_s = 5$ for a leaf incompletely covered by evaporating rain or dew. For values of r exceeding 30 s m^{-1} , surface temperatures are similar for $r_s = 0$ and 5 s m^{-1} . The theory predicts that if r_s has a finite value, however small, T_o will tend to T_a as r tends to zero. For small values of r_s , there is a regime in which surface temperature would be less than air temperature but would increase towards air temperature if windspeed decreased. For most values of r_s however, including $r_s = 0$, surface temperature decreases with increasing windspeed.

For the range of r values commonly encountered in the field, say 20 to 60 s m^{-1} for leaves, cooling as a consequence of transpiration ranges from about 1 to 2°C for $r_s = 50 \text{ s m}^{-1}$ and from 4 to 7°C when $r_s = 500 \text{ s m}^{-1}$. For a freely evaporating surface ($r_s = 0$) the corresponding range is 7.5 to 9.5°C .

The analysis of the heat balance of the equation presented here depends on two similar approximations: the relation between saturation vapour pressure and temperature is assumed to be linear; and radiative heat loss from a surface at T_o to an environment at T_a is assumed proportional to $T_o - T_a$. With these assumptions, both Δ and r_R can be calculated as functions of the known temperature T_a whereas in exact analysis, they should be evaluated at an appropriate temperature between T_a and T_o . Raschke (1958) used the same approximations to solve the heat balance equation and demonstrated that values of surface temperature so derived were almost identical to exact values obtained by solving the equation graphically. Gates & Papian (1971) and other later workers avoided the use of fixed values of Δ and r_R by determining the heat balance components iteratively with a computer. However, because they used fixed and arbitrary relationships to estimate boundary layer resistance from windspeed and leaf dimensions, all their calculations are subject to uncertainties much larger than the error introduced by the approximate solution of the heat balance equation as represented by equations 1.6 and 1.7. A few of the implications of these equations will now be considered with the help of simple graphs.

GRAPHICAL EXAMPLES

Equation 1.6 was used to calculate the excess surface temperature $T_o - T_a$ of an organ exposed to bright sunshine ($R_{ni} = 300 \text{ W m}^{-2}$) with $T_a = 20^\circ \text{C}$ and $\delta = 10 \text{ mbar}$, values characteristic of a summer day in a temperate climate (Fig. 1.6). The independent variable was r , the resistance for heat and mass transfer by convection as determined from Table 1.1 or Fig. 1.2, for example.

For a non-transpiring surface ($r_s = \infty$), $T_o = T_a$ when $r_a = 0$ and ($T_o - T_a$) increases linearly with the total thermal resistance $r_t = (r^{-1} + r_R^{-1})^{-1}$. The increase with r is therefore non-linear as shown and in the limit when r is very large $T_o - T_a$ tends to the value $r_R R_{ni} / \rho C$ or 52°C in this example.

For a perfectly wet surface ($r_s = 0$), the minimum value of T_o is the wet-bulb temperature and $T_o - T_a$ is given by $\delta e / (\Delta + \gamma)$.

Curves for three finite values of r_s are also shown. The value $r_s = 50 \text{ s m}^{-1}$ corresponds to a leaf with stomata wide open and in this environment $T_o - T_a$ is almost proportional to r . Since the convective heat flux C is proportional to $(T_o - T_a)/r$ (eqn 1.3) it follows that C must be nearly independent of r which implies that $\lambda E (= R_n - C)$ is also nearly independent of r . It is shown elsewhere (Monteith 1965) that the exact condition for evaporation rate to be independent of windspeed is $\lambda E / C = \Delta / \gamma$ which implies that $r_s = \rho C \delta (\Delta + \gamma) / \Delta \gamma R_n$. When r_s is greater than this critical

Figure 1.7 shows the corresponding calculation of $T_o - T_a$ at night when $R_{ni} = -100 \text{ W m}^{-2}$ and $T = 10^\circ\text{C}$. The line marked 'dry' corresponds to a system in which there is no condensation so that $R_n = C$. For a surface wetted by dew, eqn 1.7 is valid with $r_s = 0$. Cooling of the surface below air temperature is least when the atmosphere is saturated (dew 100). Dew may form when the atmosphere is unsaturated but only when the resistance exceeds a limiting value, e.g. about 25 s m^{-1} for a relative humidity of 90% in the example shown. In the very light winds usually associated with dew formation, the boundary layer resistance of leaves is expected to fall between 50 and 100 s m^{-1} implying that the rise in temperature attributable to the release of latent heat is of the order of 1.5 to 3°C . When the air temperature is close to 0°C , this rise will sometimes be sufficient to prevent, or at least to delay, damage to tissue by freezing.

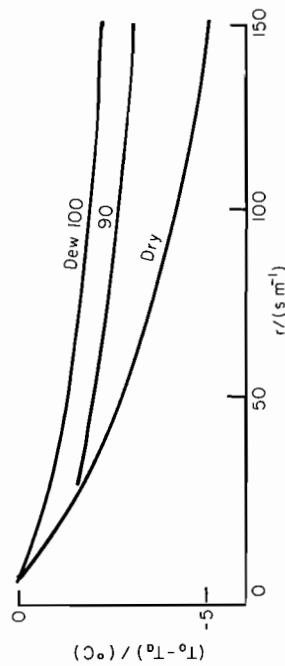


FIG. 1.7. Predicted difference between surface and air temperature for a leaf with specified boundary layer resistance in the dark ($r_s = \infty$). Assumed microclimate: $R_{ni} = -100 \text{ W m}^{-2}$; $T = 10^\circ\text{C}$. Dew formation occurs when r.h. is 100 or 90%. The 'dry' curve is appropriate when the r.h. is too low to allow condensation.

Salisbury & Spomer (1964) and other workers have noted that the leaf temperature excess in bright sunshine tends to be high when the leaf temperature is low and vice versa. This effect can be predicted from eqn 1.6 on two grounds.

- (i) Because Δ increases with temperature, ($T_o - T_a$), if positive, will tend to decrease with increasing temperature.
- (ii) For a fixed relative humidity, the saturation deficit δ increases with temperature. Figure 1.8 shows the relation between $T_o - T_a$ and T_a for a leaf with $r = r_s = 50 \text{ s m}^{-1}$ exposed to radiation at 300 W m^{-2} . The upper line corresponds to a relative humidity of 70%, characteristic of the level often recorded in crop canopies. The lower line corresponds to much drier air at 35% r.h. Fortuitously, both relations are almost linear, and their slopes are about -2.2 and -3.1 . The effect of strong radiative heating at low air temperatures may be particularly significant for arctic and for alpine communities as observed by Warren Wilson

(1957) and others. In the tropics, on the other hand, a leaf adapted to keep stomata open when air temperature is $30\text{--}40^\circ\text{C}$ should be able to maintain its tissue at a similar temperature. Linacre (1964a) suggested that observed leaf temperatures were usually below air temperature when $T_a \approx 35^\circ\text{C}$, but the calculation presented here shows that the critical temperature for $T_o = T_a$ must be a function of several micro-meteorological variables and of stomatal resistance.

Attention has recently been focused on the tendency for the leaves of some species to reduce stomatal aperture in response to an increase of saturation deficit and therefore of potential transpiration rate. The analysis considered here shows that a modest degree of stomatal closure is unlikely to cause overheating of very small leaves such as coniferous needles, in any climate, or of any leaves exposed to high air temperatures.

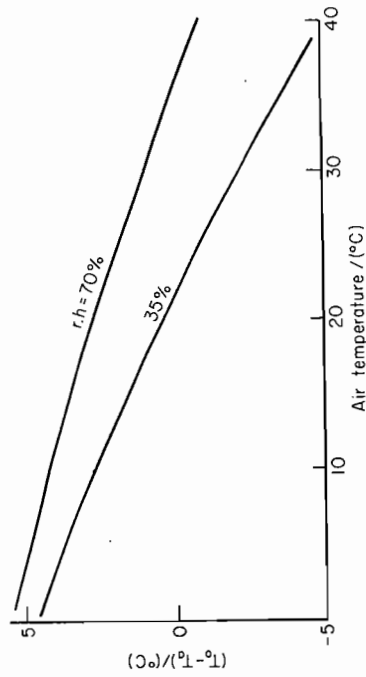


FIG. 1.8. Predicted difference between leaf surface and air temperatures as a function of air temperature at two specified levels of relative humidity. Assumed microclimate $R_{ni} = 300 \text{ W m}^{-2}$, $r = r_s = 50 \text{ s m}^{-1}$.

THERMAL CAPACITANCE

In a previous section, an expression was derived for $T_o = T_e$, the mean surface temperature of an organ in thermal equilibrium with its environment. When T_e changes as a result of a change in radiation, windspeed, air temperature or humidity, surface temperature cannot change instantaneously but must lag behind the change in T_e to an extent which depends on the heat capacity of the organ and on other factors now considered.

Suppose the mean surface temperature of an organ is $T \neq T_e$ so that the organ gains heat from the environment at a net rate given by

$$R_n - C - \lambda E = R_{ni} - \frac{\rho c(T - T_a)}{r_t} - \frac{\rho c[e_s(T) - e_a]}{\gamma^* r_t} \quad (1.13)$$

$$= \mathbf{R}_{ni} - \frac{\rho c(T - T_a)}{r'_i} - \frac{\rho c \delta}{\gamma^* r_i} \quad (1.13a)$$

where r_i , r'_i and γ^* are defined in equations 1.10–1.12. By definition, the gain of heat from the environment becomes zero when $T = T_e$, i.e.

$$0 = \mathbf{R}_{ni} - \frac{\rho c(T_e - T_a)}{r'_i} - \frac{\rho c \delta}{\gamma^* r_i} \quad (1.13b)$$

Subtracting eqn 1.13b from eqn 1.13a, the gain of heat when $T = T_e$ is

$$\mathbf{R}_n - \mathbf{C} - \lambda E = \rho c(T_e - T)/r'_i \quad (1.14)$$

The rate of gain of heat can also be expressed in terms of the rate at which the heat content of the organ increases. With the important proviso that the whole organ is at a uniform temperature T , the rate of change of heat content can be written as $(\rho'c'v/A)\dot{T}$ where $\dot{T} = \partial T/\partial t$, $\rho'c'$ is the volumetric heat capacity and v is the volume of tissue with an external area of A (one side only for a leaf). The heat balance of the organ is therefore given by

$$\rho c(T_e - T)/r'_i = (\rho'c'v/A)\dot{T} \quad (1.15)$$

which can be reduced to the form

$$\dot{T} = (T_e - T)/\tau \quad (1.16)$$

where τ , with dimensions of time is given by

$$\tau = r'_i(\rho'c'/\rho c)(v/A) \quad (1.17)$$

For a leaf, the term v/A is simply a mean thickness. For a stem, treated as an infinite cylinder of diameter d , it is $d/4$ and for a sphere it is $d/6$.

Unfortunately, values for the heat capacity of plant tissue are extremely hard to find in the literature. According to Miller (1938), measurements of intercellular space in leaves range from 3 to 70% of tissue volume, and assuming that the tissue is composed entirely of water with a specific heat of $4.2 \text{ J g}^{-1} \text{ K}^{-1}$, the corresponding range of volumetric specific heat is 4.1 to $1.3 \text{ MJ m}^{-3} \text{ K}^{-1}$. For an intermediate value of $3 \text{ MJ m}^{-3} \text{ K}^{-1}$ and with $\rho c = 1.2 \text{ kJ m}^{-3} \text{ K}^{-1}$ for air at 20°C , $(\rho'c'/\rho c) \approx 2.5 \times 10^3$. The specific heat of fruit depends mainly on fractional water content (Turrell & Perry 1957) and a range from 2 to $3 \text{ MJ m}^{-3} \text{ K}^{-1}$ is probably appropriate. For wood, the range of specific heat must be substantial because the density of wood ranges from 0.1 t m^{-3} for balsa to 1.33 t m^{-3} for ebony (Weast 1977). Furthermore, large differences of specific heat are associated with the radial differences of water content observed in tree trunks. For example, Herrington (1969) found that $\rho'c'$ for red pine increased from $0.9 \text{ MJ m}^{-3} \text{ K}^{-1}$ in the heartwood to $2.6 \text{ MJ m}^{-3} \text{ K}^{-1}$ in sapwood with a mean value of $2.0 \text{ MJ m}^{-3} \text{ K}^{-1}$ for the whole trunk.

Eqn 1.16 is formally identical to the expression for the rate of change of voltage V across a capacitance C in series with a resistor R . When a voltage E is imposed across the components, the subsequent change of V is given by

$$\dot{V} = (E - V)/RC \quad (1.18)$$

and \dot{V} decreases as the condenser accumulates charge. The term RC is known as the 'time-constant' of the circuit and this name is appropriate for τ .

The voltage across the condenser increases from $V = 0$ to a maximum value of E . In the same way, the temperature of an organ will always move in the direction of an equilibrium temperature at which $T = T_e$, i.e. the excess of surface over air temperature will tend to the value given in eqn 1.6. Fig. 1.9 is an analogue circuit which is electrically equivalent to the circuit of Fig. 1.5. The battery imposes a voltage of $\rho c(T_e - T)$ across a resistor r'_i and a capacitor C in series. As the time constant of the circuit τ is the product $r'_i C$, the thermal capacity can be identified as $\tau/r'_i = (\rho'c'/\rho c)(v/A)$ which has dimensions of length.

To indicate scale, time constants were calculated for plant organs of different shape and size and for two windspeeds, assuming $\rho'c'/\rho c = 2.5 \times 10^3$. Table 1.2 shows that the value of τ for small leaves is of the order of a few seconds (and is therefore difficult to measure accurately). For larger leaves, τ ranges from the order of a minute for a characteristic dimension of 5 cm to several minutes for very large leaves. Stems, buds and fruits have a larger range of τ because their volume/area factor is larger. Even for small twigs and berries, τ is of the order of 1 min and for the trunks of mature trees and very large fruits τ is a significant fraction of 1 day.

TABLE 1.2. Time constants for leaves, stems and fruits treated as simple geometrical shapes. r'_i is calculated from eqns 1.1 and 1.10 and τ from eqn 1.17. Values are for non-transpiring organs except those in brackets which were calculated from leaves with $r_s = 50 \text{ s m}^{-1}$ at 20°C .

	Arbitrary dimensions		Time constant (minutes)	
	d	(v/A)	1	4
Leaves				
grass	0.6	0.05	0.22 (0.16)	0.11 (0.10)
beech	6	0.10	1.13 (0.63)	0.66 (0.43)
giant hogweed	60	0.15	3.50 (1.61)	2.35 (1.21)
Stems, etc.				
bramble	0.6	0.15	1.73	0.81
whin	6	1.5	37	18.8
beech trunk	60	15	650	390
rowan	0.6	0.1	0.85	0.39
crab apple	6	1	18.7	9.2
Jack fruit	60	10	360	200

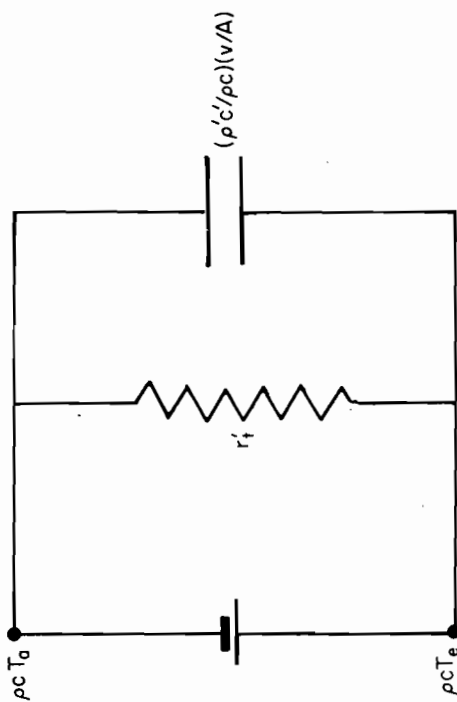


Fig. 1.9. Electrical circuit analogous to dynamic heat balance of leaf and for the same leaf (eqn 1.15).

The ratio of time constants for a transpiring leaf and for the same leaf in the same environment with stomata closed is

$$r_i'/r_i = (1 + \Delta/\gamma^*)^{-1} \quad (1.19)$$

For a completely wet surface ($r_s = 0$), r_i'/r_i has a value of about 0.3 at 20°C, and this ratio describes the relative response times of a wet and dry bulb thermometer of the same size. For a leaf with $r_s \approx r$, a common condition, $r_i'/r_i = 0.5$ at 20°C.

Solutions of the dynamic heat balance equation

Equation 1.16 can be solved for a number of standard boundary conditions to obtain surface temperature as an explicit function of time. For example, if the equilibrium temperature T_e increases (or decreases) instantaneously from T_1 to T_2 as a result of a change in T_a , R_n or δ , the surface temperature will increase (or decrease) exponentially as shown in Fig. 1.10a. The corresponding solution is

$$T = T_2 - (T_2 - T_1) \exp(-t/\tau) \quad (1.20)$$

This equation is appropriate for a leaf exposed to sudden changes of irradiance when small clouds obscure the sun. The response time of a leaf which has been shaded can be estimated by measuring the mean surface temperature as a function of time and plotting $\ln[(T_2 - T)/(T_2 - T_1)]$ against t to give $-1/\tau$ as a slope. Linacre (1964b) and others have used this method to estimate heat transfer coefficients which are inversely proportional

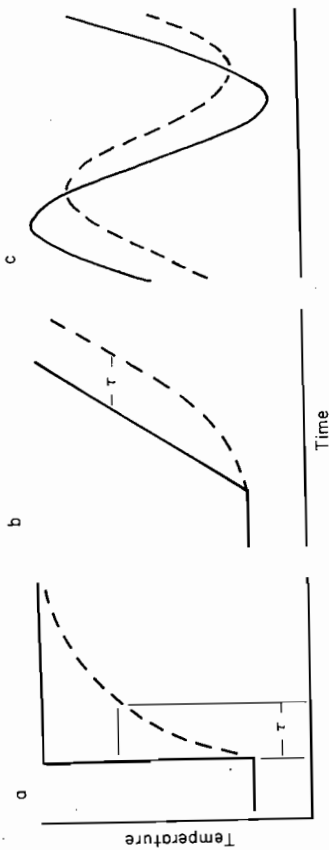


Fig. 1.10. Change of surface temperature (dashed line) in response to change of environmental temperature (full line). (a) Step change (eqn 1.20); τ is the time for a fractional change of $1 - e^{-1}$ or 0.63. (b) Ramp change (eqn 1.23); τ is the constant time lag established after the term $\exp(-t/\tau)$ becomes negligible. (c) Harmonic oscillation for the case $\omega\tau = 1$ (eqns 1.25, 1.25a and b).

to τ , but the way in which transpiration reduces the effective time constant, as shown by equation 1.17, has usually been ignored.

By combining equations 1.19 and 1.20, it is possible, at least in principle, to determine both r and r_s for a leaf, using a stopwatch and a radiation thermometer or a carefully installed set of thermocouples. The leaf must first achieve a constant measured temperature in sunshine. It is then shaded and the change of temperature with time recorded so that the 'wet' time and the change of temperature from equation 1.20. The leaf is then covered with vaseline to stop transpiration and the shading process is repeated to find the 'dry' constant τ_d (Linacre 1972). Since $\tau_w/\tau_d = (1 + \Delta/\gamma^*)^{-1}$, it can be shown from the definition of γ^* that

$$r_s/r \approx \{(\Delta/\gamma)/[(\tau_d/\tau_w) - 1]\} - 1 \quad (1.21)$$

when $r_i \approx r$. If the mean thickness x of the leaf is measured, r can be calculated as $\tau_d/(\rho'c'/\rho c)x$ so that r_s can be estimated from equation 1.21. (In some circumstances the estimate would not be very exact but the procedure is worth noting as an instructive exercise.)

A second case is illustrated in Fig. 1.10b, where the equilibrium temperature changes at a constant rate α from an initial temperature T_1 . The boundary condition is

$$T_e = T_1 + \alpha t \quad (1.22)$$

and the corresponding solution of equation 1.16 is

$$T = T_1 + \alpha(t - \tau) + [\alpha\tau \exp(-t/\tau)] \quad (1.23)$$

The term in square brackets can be neglected when $t > 2\tau$ and thereafter the temperature of the organ increases at the same rate as air temperature

but with a time lag $\alpha\tau$. Monteith & Butler (1979) used this equation to calculate the surface temperature of cocoa pods on which dew may form after dawn when the surface temperature rises more slowly than the dew-point of the surrounding air.

A harmonic oscillation of temperature (Fig. 1.10c) has the form

$$T_e = \bar{T}_e + A \sin \omega t \quad (1.24)$$

where \bar{T}_e is a mean equilibrium temperature with maximum and minimum values of $\bar{T}_e \pm A$ and ω is the frequency of the oscillation equal to $2\pi/P$ where P is the period. The appropriate solution of eqn 1.16 is

$$T = \bar{T}_e + A' \sin(\omega t - \varphi) \quad (1.25)$$

where the semi-amplitude of the surface temperature is

$$A' = A \cos \varphi \quad (1.25a)$$

and the phase lag is

$$\varphi = \tan^{-1}(\omega\tau) \quad (1.25b)$$

which has a maximum value of $\pi/2$ or 6 h for a 24 h cycle. In principle, this type of analysis can be used to predict how the surface temperature of an organ should respond to a diurnal oscillation of T_e . For organs such as leaves, buds and small fruits, τ is much smaller than ω^{-1} which has a value of $P/2\pi$ or about 4 h when $P = 24$ h. When the product $\omega\tau$ is small, the amplitude of surface temperature A' is close to the imposed value of A and the phase lag φ is negligible. For very bulky organs such as tree trunks, τ and ω^{-1} are of comparable magnitude so that the simple theory represented by eqn 1.25a predicts that A' may be substantially smaller than A . In rigorous analysis, however, the temperature gradients which exist within large organs cannot be neglected as they were in deriving eqn 1.16 and this point is considered in the next section.

The ecological significance of the thermal time constants which are characteristic of plant organs has received little attention but in terms of adaptation the response to rapid or systematic changes of environmental temperature may be just as important as differences in thermal resistance discussed by Lewis (1972) and others.

In an environment where there is a risk of damage to tissue by extremes of heat or cold, large organs are likely to survive stress more readily than small ones. It is possible, for example, that giant cacti maintain internal temperatures which are well below air temperature and surface temperature in bright sunshine. Large organs also avoid the effect of very short periods of high or low temperature often associated with a brief drop in windspeed. Low growing arctic and alpine species may achieve similar protection because they are thermally coupled to the underlying soil rather than to the atmosphere (see Grace, this volume).

When microclimate and species are matched so that rates of physiological processes increase more or less linearly with temperature, the mean rate over a whole day will be independent of the range of tissue temperature. But when the relation between rate and temperature is *not* linear, the mean rate for the day will depend on the details of its thermal history and not simply on the mean temperature. In the tropics, environmental temperature T_e around midday may exceed the optimum for photosynthesis, particularly for plants which are short of water. Thermal inertia as a result of a large mass could be an advantage if it postponed the time of maximum tissue temperature until air temperature started to decline in the middle of the afternoon. This argument is contrary to the widespread view that small leaves are well adapted to survive in high air temperatures and bright sunlight. In fact, many tropical species are notable for the large size of their leaves whereas many temperate and arctic species have relatively small leaves.

When vegetation is exposed to fire, the thermal response time of essential tissue must be an important factor in the survival of species. In a textbook reviewing the effects of fire on ecosystems (Kozlowski & Ahlgren 1974) this aspect of environmental physics is referred to briefly but is not treated quantitatively.

CAVEAT — LACK OF UNIFORMITY

The calculations of heat transfer and rate of temperature change in the last section were based on the assumption that the tissue within a plant organ can be treated as isothermal. In practice, this condition is not always satisfied and the existence of temperature gradients has a number of implications.

In the first place, the formula for the thermal resistance of a flat plate (eqn 1.1 and Table 1.1) is appropriate for a surface with uniform temperature. In laminar flow, the loss of sensible heat per unit area from such a surface decreases with the square root of distance (x) from the leading edge. When heat flux rather than temperature is uniform over the surface, the temperature excess decreases with $x^{1/2}$ as Wigley & Clark (1974) demonstrated for a model leaf.

In practice, for a given mean temperature excess the difference in flux between the two cases is small. The value of A in the constant flux equation is about 10% of the 'isothermal' value in Table 1.1 and the value of n is the same. A real leaf within a canopy will tend to behave like a constant flux surface when the whole lamina is in bright sunshine but when part of the lamina is shaded, the distribution of flux and of temperature is complex. Fortunately, the thermal coupling of leaves to their environment appears to be unaffected by the fact that sensible heat transfer occurs over the whole epidermis whereas latent heat is lost mainly from tissue surrounding the substomatal cavity (Cowan 1972b).

For any curved element of surface on a fruit or tree trunk, for example, the boundary layer resistance depends on the direction of the airflow whereas the irradiance is a function of orientation with respect to the sun and sky. Tanner & Golz (1972) measured the temperature of ovaries attached to the umbel of onions and observed the maximum difference between ovary and air temperature over the segment directly facing the sun. The excess temperature was greatest when this segment was at right angles to the direction of the wind and decreased by a factor of about 5 when the segment was facing into the wind. For a fixed angle between sun and wind, the excess temperature was inversely proportional to $u^{2/3}$ and exceeded 15°C when u fell below 1 m s⁻¹. It was suggested that ovary temperatures of 50 to 60°C could be responsible for loss of seed production.

Very few systematic measurements or estimates of internal temperature have been published. Thorpe (1974) calculated the temperature distribution inside a sunlit apple and predicted that when radiant energy was absorbed at 500 W m⁻², the excess of tissue temperature above air temperature would be 9°C just below the skin at a point facing the sun, 4°C at the centre and 2°C at the coolest point on the surface. Although the theory took no account of differences in boundary layer thickness associated with wind direction, similar measurements of surface temperature were obtained with a radiation thermometer. The thermal time constant for a change in irradiance was about 10 min at a point facing the sun and this figure is consistent with an estimate from eqn 1.17. The time constant was more than 1 h at the centre of the fruit.

Herrington (1969) solved the equations for the radiant flow of heat in a tree trunk and compared predicted changes of temperature with measurements in the stem of a 48 year old specimen of *Pinus resinosa* in a plantation. He used a mean value of volumetric specific heat in the analysis but the measured value increased by a factor of three between the heartwood and the cambium. In contrast to the system studied by Thorpe, the trunk was not exposed to bright sunlight so there was no significant difference in surface temperature around the trunk and diurnal changes of internal temperature agreed well with theory. The amplitude of surface temperature was 0.75 of the air temperature amplitude compared with a value of 0.63 from eqn 1.25a but in the centre of the trunk the relative amplitude was only 0.25. The measured phase lag was 0.6 h at the surface increasing to 9.3 h at the centre of the trunk compared with a value of about 3 h from eqn 1.25b.

From the comparison of elementary theory assuming uniform tissue temperature (eqn 1.16) and the more exact analyses of Thorpe and Herrington, it appears that eqn 1.25 provides a good estimate of *surface* temperature amplitude even for bulky organs but substantially overestimates the amplitude within the tissue. The phase lag derived from simple theory (eqn 1.25b)

overestimates the lag at the surface and underestimates the lag at the centre of a tree trunk or a large fruit.

OTHER FORMS OF COUPLING: BRIEF CRITIQUE

At least two other forms of coupling between plants and the atmosphere have been represented by electrical analogues. The treatment of water flow as a current passing through a resistance was referred to in the introduction. Measurements have shown, however, that the resistance (R) often decreases with increasing flow rate (i) (Weatherley 1976) and in the limit when $R \propto 1/i$ the 'resistance' becomes a constant potential device. Similarly, the water capacity of plants (C) defined as a change in water content per unit change of potential is not a unique property of the tissue but changes with the value of the potential (Milburn 1979). Several workers have analysed diurnal changes of plant water potential using an equation of the form

$$\psi = (\psi_0 - \psi)/RC$$

where ψ_0 is a constant base potential. Wallace (1978) found that the hydraulic time constant (RC) for a stand of winter wheat fluctuated between 30 and 110 min during the summer of 1975 and Jones (1978) reported an even wider range from 17 min to 174 min for three varieties of wheat growing in three seasons. In neither analysis could the variability of RC be related to age, weather, soil water history or morphology and it is doubtful whether the concept of a unique time-constant is valid in a circuit whose components are functions of current and potential. More complete models have been developed in which individual organs are represented by separate R - C circuits (Powell & Thorpe 1977; Meidner & Sherriff 1976) but the validity and usefulness of such analogues remain to be demonstrated.

The awkwardness of non-linear components has also inhibited the development of resistance analogues of photosynthesis and respiration. In the most elementary models of photosynthesis, the resistance to CO₂ diffusion is expressed as the sum of three components: the boundary layer and stomatal resistances already discussed and a 'mesophyll' resistance r_m often evaluated as a residual term (Jarvis 1971; Unsworth, this volume). The mesophyll resistance can be treated as the sum of a physical resistance for CO₂ diffusion in the liquid phase and a chemical quasi-resistance determined by the kinetics of the photochemical process; but neither of these components can be readily measured or estimated. Unlike conventional resistances, the so-called carboxylation component of the chemical resistance is proportional to the local potential. Moreover, the derivation of a carboxylation resistance from the shape of a light response curve (Prioul & Chartier 1977) is based

on the implicit but implausible assumption that the physical sector of the CO₂ diffusion pathway is identical for all cells.

Resistance models of respiration have also been proposed (Lake 1967). Ryle, Cobby & Powell (1976) showed that the respiration of labelled carbon from maize and barley plants decreased at a rate which could be represented by two time constants, one of about 7 to 11 hours and the other about 4 to 5 days. Respiration could therefore be represented by the discharge of two RC circuits but as the rate of discharge is effectively independent of the inter-cellular CO₂ concentration, it is difficult to see how an R-C model of respiration could be coupled to a resistance model of photosynthesis.

Despite these limitations, electrical analogues of CO₂ coupling provide a useful complement to similar analogues of water vapour coupling, particularly for estimating the rate of water transpired per unit of carbon assimilated (Penman & Schofield 1951; Rijtema 1968). Cowan & Farquhar (1977) have suggested that this ratio may be optimized by diurnal changes of stomatal resistance—a highly sophisticated form of coupling between plants and the atmosphere. Supporting evidence comes from Goudriaan & van Laar (1978) who found that the stomatal resistance of some species tends to change in a way which stabilizes the intercellular CO₂ concentration.

Electrical analogues have also been useful in establishing the relative importance of the resistances which couple plant leaves to their CO₂ supply. The mesophyll resistance usually dominates the circuit so that the rate of carbon assimilation changes less than transpiration when stomata close and is usually independent of windspeed. In a few experiments, however, the dependence of CO₂ assimilation on boundary layer resistance has been clearly demonstrated (e.g. by Yabuki & Miyagawa 1970) and this aspect of coupling deserves closer attention in field studies.

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2. SOME EFFECTS OF WIND ON PLANTS

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SUMMARY

1. Field observations suggest that wind affects the shape and size of trees, the physiognomy of the vegetation, and the productivity of crops. Ecologists and foresters use the term 'exposure' to describe this impact of wind on vegetation. The present article explores the physical and biological meaning of this term.
2. Transport of heat, gases and momentum across the boundary layer between the atmosphere and the plant depend on structural features of the vegetation. High transport rates between plant surfaces and the air occur when the leaves, stems and branches are small rather than large, and when the vegetation is tall rather than short. In parts of the world where overall temperatures are low and windspeeds high it is argued that, if all other variables are equal, tall or small-leaved plants will be colder than short or broad-leaved plants, and so be at a disadvantage.
3. The effect of wind on transpiration can be calculated from the Penman-Monteith equation. Wind does not always increase transpiration rate: in many ordinary conditions an increase in wind causes a decrease in transpiration.
4. Leaf surfaces may sustain damage in wind, causing a disruption of proper cuticular control of water loss. This damage has been observed in grasses, *Acer* and *Fragaria* but does not seem to occur in conifers.
5. The effect of wind on exchanges of gases can be calculated if the other (physiological) resistances in the total diffusion path are known. In general, the effect of wind on the rate of photosynthesis is small (except at very low windspeeds), because the stomatal and mesophyll resistances are large in relation to the boundary layer resistance.
6. There are several reports which suggest that motion *per se* is a potent inhibitor of plant growth. The mechanisms involved are unknown.
7. In conclusion, the shaping of trees by the wind and the general effects of 'exposure' already referred to are likely to be caused by the effect of wind on the temperature of leaves and meristems, damage to leaf surfaces, and the direct effect of motion as an inhibitor of growth.

INTRODUCTION

Effects of wind on vegetation may be seen almost everywhere. Trees growing in windy places are often shaped by wind, their branches appearing permanently swept to the leeward, earning the names 'wind-brushed' or 'flag tree', and these shaped trees have even been used to assess the average strength and direction of the wind (e.g. Putnam 1948; Sekiguti 1951; Holroyd 1970; Yoshino 1973; Wardle 1977). The extreme condition occurs at the

altitudinal limit of tree growth, where tree species may adopt a prostrate form—the 'krummholz' condition (Wardle 1968).

Effects like these are not confined to trees. At high altitudes, above the treeline, the shrub vegetation is locally dwarfed. Many years ago Raunkiaer (1909, 1934) proposed a functional classification of plants, defining certain 'life forms' on the basis of height above the ground of their perennating organs. He showed that cold and windy areas supported only a restricted spectrum of life forms—those with buds near the ground. Similarly, Tansley (1939) showed that above 1000 m a.s.l. in the Scottish Grampian mountains, 27 per cent of the species are chamaephytes as compared to 9 per cent in the flora of the world as a whole; and Gimingham (1951) demonstrated a similar shift towards dwarf and prostrate growth forms with increasing exposure to the wind in sand dune systems.

TABLE 2.1. The spectrum of growth forms at sites of increasing exposure to the wind on Monte Maiella, Italy (site A is most exposed). Figures refer to % of total vegetation at that site (from Whitehead 1954).

Growth form	Site exposure to the wind			
	D	C	B	A
Medium herb, 100 mm	1.56	—	—	—
Small sub-shrub, 50 mm	0.82	—	—	—
Small herb, 50-100 mm	5.04	4.03	—	—
Large tussock, diam. 500 mm	18.1	3.07	—	—
Large cushion, diam. 50 mm	9.14	20.3	—	—
Woody mat	58.0	22.0	0.30	—
Herbaceous mat	—	5.68	21.1	—
Large rosette, diam. 50 mm	4.55	6.90	30.2	—
Small rosette, diam. 50 mm	0.67	7.40	8.45	6.02
Small tussock, diam. 50 mm	0.01	0.67	8.59	4.30
Small cushion, diam. 50 mm	2.36	2.2	6.03	30.4
Prostrate, suffruticose or woody	—	—	5.73	15.7
Prostrate herb	—	—	19.6	43.5

In two most interesting papers Whitehead (1954, 1959) described the influence of creating shelter around small plots of mountain vegetation with walls of stones (Table 2.1). Over just one year the resulting shelter increased the average plant height from 22 mm to 32-68 mm. In later years new species invaded the sheltered plots and the percentage cover of established species changed markedly. More recently Nägeli (1971) showed a similar dependence of vegetation type on wind speed in an alpine valley; he demonstrated that the natural shelter afforded by topography created physiognomic differences in the vegetation.

Shelter is also significant to agricultural production. Since the early

work of Bates (1911) there have been many demonstrations that shelter belts or windbreaks increase the yield of crops. In a recent review covering eighty-six different cases, substantial improvements in the yield (>10%) of the crop, attributable to shelter, were reported in sixty-eight cases (Grace 1977).

How are these effects to be interpreted? Ecologists and foresters have used the word 'exposure' to describe the combined stresses that plants suffer in cold and windy places. The word has been used in a rough and intuitive manner and 'exposure' is rarely defined in a measurable way. Yet our knowledge of microclimates and the aerodynamics of vegetation has advanced considerably in recent years, to the point where we ought now to understand the meaning of this 'exposure'. Electric resistance models have provided a focal point whereby knowledge from the physical and engineering sciences may be brought to bear on biological problems and, in particular, on the estimation of transpiration rates and surface temperatures. This chapter brings together some recent advances in the general field of wind relations so that the concept of 'exposure' may be reassessed.

EXCHANGES IN THE BOUNDARY LAYER

The important role of air movement is to ventilate plant surfaces, mixing air near the leaf with new air from the bulk of the atmosphere. Hence, in conditions of bright sunlight, fresh supplies of carbon dioxide are brought to the leaves, while water vapour and heat are transported away.

The basic equation which expresses the transfer of any entity between a surface and the atmosphere states that the flux is proportional to the concentration gradient.

$$F = -D \cdot \delta x / \delta z \quad (2.1)$$

where F is the flux, $\delta x / \delta z$ is the vertical concentration gradient above the surface and D is a transfer coefficient, in appropriate units.

If the flow of air is laminar, the appropriate value for D is the molecular diffusivity. In many other circumstances, the flow of air is turbulent and the appropriate transfer coefficient is that of eddy diffusion, K . In general, values of K are highly variable and always larger than the coefficients of molecular diffusion. Within vegetation K may vary from 10^{-5} near leaves to $10^{-1} \text{ m}^2 \text{ s}^{-1}$ near the top of the plants, while above the crop K increases linearly with height and may be as high as $10^2 \text{ m}^2 \text{ s}^{-1}$. This large variation occurs because the size of the individual eddies, which are the medium for transport, increases with height above the surface. In such a medium the rate of transport is independent of molecular size, and so, according to the principle of Prandtl, the value of K is independent of the entity being transported.

A diffusion resistance r , or its inverse the conductance g , is defined in

relation to vertical distance z as

$$r = g^{-1} = \int_{z_1}^{z_2} \frac{dz}{D} \quad (2.2)$$

Thus if we consider diffusion from a hairy leaf, a layer of still air trapped by dense hairs 1 mm long might be expected to impose a resistance to water vapour diffusion of $1 \times 10^{-3} / (2.4 \times 10^{-5}) \approx 40 \text{ s m}^{-1}$. This is equivalent to half a metre or so of turbulent air, assuming $K = 10^{-2} \text{ m}^2 \text{ s}^{-1}$ above the leaf.

When is the flow of air over the leaves laminar and when turbulent? Classical studies in fluid dynamics suggest that this question may be answered if the Reynolds number Re is known:

$$Re = \frac{ul}{\nu} \quad (2.3)$$

where u is the fluid velocity, l is the characteristic dimension of the test object—for a leaf it would be the average length in the direction of the airflow, and ν is a property of the fluid called the kinematic viscosity. At low values of Re the fluid moves as a coherent mass because of its viscous properties. As Re rises above a critical point Re_{crit} the inertial forces within the fluid predominate and the smooth flow breaks down to give chaotic motion in which individual lumps of fluid move in directions other than parallel to the main flow and mixing occurs.

For smooth flat plates exposed to laminar flow in a wind tunnel the transition from a laminar to a turbulent boundary layer occurs at a Reynolds number of about 2×10^4 . As Reynolds numbers for leaves in natural conditions are less than this, the view has arisen that the air flow over leaves must be laminar (Oke 1977), and that the theory of laminar boundary layers may be used in any calculations. However, when the air flow over real leaves has been investigated the boundary layer is seen to be turbulent (Perrier *et al.* 1973; Grace & Wilson 1976). For example over a *Populus* leaf exposed in a wind tunnel to smooth air flow at 1 m s^{-1} the boundary layer was laminar only for a short distance along the adaxial surface (Fig. 2.1). Elsewhere there was considerable turbulence, which seemed to originate from surface irregularities such as veins standing proud, or the decurrent leading edge (Fig. 2.1). The critical value of Re needed for the transition from laminar to turbulent flow seems to be between 400 and 3000, much lower than those normally quoted in engineering texts which refer to smooth flat plates. Turbulence in the boundary layer is encouraged by turbulence in the air stream incident on the leaf, and accentuated by the uneven topography and roughness of the leaf. Decurrent leading edges, or a serrated margin may serve to 'trip' the airflow and so precipitate turbulence.

These measurements suggest that the boundary layers over leaves are usually turbulent or partly turbulent when the wind blows, except in the very

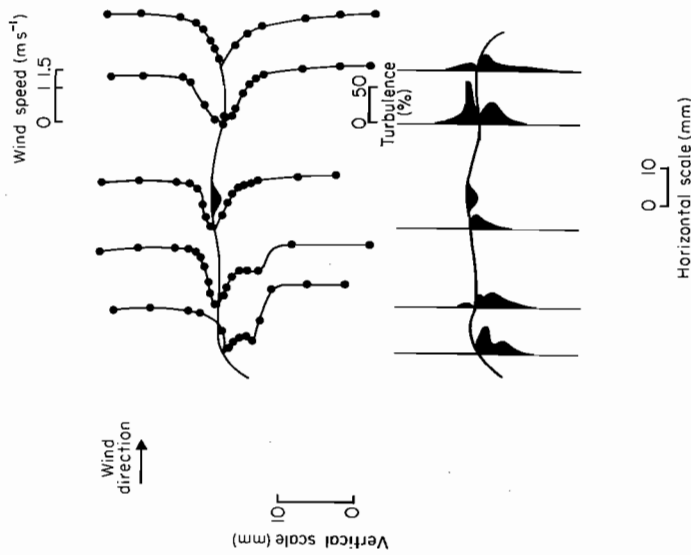


FIG. 2.1. Profiles of mean wind speed (*upper*) and turbulence (*lower*) around a *Populus* leaf shown in transverse section. The free air-stream in the wind tunnel was laminar, but the boundary layer was turbulent over much of the surface. The scale for height is exaggerated X2 compared to the horizontal scale for length (from Grace & Wilson 1976).

low wind speeds and in the case of very small leaves where the dimension is so low as to give a very small Reynolds number. It should be realized that even in a fully-developed boundary layer there is a *viscous sublayer* very close to the surface in which the flow remains laminar. Some idea of the thickness of this sublayer can be obtained by observing the motion of minute objects which happen to occur at the leaf surface, such as fungal conidiophores. From one series of experiments the sublayer would appear to be not more than a few tens of micrometres though in hairy leaves it might be considerably more (Grace & Collins 1976).

EFFECT OF WIND SPEED ON r_a OF LEAVES

Attempts to measure the effect of wind speed on the boundary layer resistance r_a have been made many times. The most common method has been to make a paper model of the leaf, wet it with water, and then measure the evaporation rate of water from it in an airstream of known humidity (Jarvis 1971). Calculation of the resistance requires an estimate of the water vapour

pressure at the evaporating surface; this value is very sensitive to any small differences in temperature over the surface. Moreover, it is not always easy to maintain the air flow at a constant and known humidity (for a discussion of errors see Grace & Wilson 1976). These problems have led some workers to use completely different diffusing species (Thom 1968; Macleod & Todd 1973; Chamberlain 1974).

There is perhaps a larger source of error in this procedure; leaf microtopography cannot be represented in the paper model. In a real leaf much of the resistance to transfer may reside in the sublayer trapped between hairs, grooves or papillae.

Boundary layer resistance has been measured by engineers as well as by plant scientists. Many fluids other than air have been used, and surfaces of diverse size and shape have been employed according to the needs of the investigator. It is useful to be able to bring results from all these experiments together to make 'predictive' formulae: this may be done using *dimensionless groups* to express the transfer rates (see also the papers in this volume by Monteith, Chamberlain and Proctor). The application of dimensionless groups is discussed in textbooks on heat and mass transfer and also by Monteith (1973), Leyton (1975) and Campbell (1977); there follows a definition of the dimensionless numbers which are used universally to describe mass and heat transfer. To express mass transfer we use the Sherwood number *Sh*

$$Sh = \frac{F l}{D(\chi_s - \chi_a)} \tag{2.4}$$

where *F* is the mass flux density (kg m⁻² s⁻¹), *l* is the dimension of the object parallel to the wind speed (m), *D* is the appropriate coefficient of molecular diffusion (m² s⁻¹), χ_s is the concentration at the surface and χ_a is the concentration in the bulk of the fluid (kg m⁻³). The more familiar boundary layer resistance can be found as $r'_a = 1/DSh$ where the suffix ' is used to denote that this is for one side of the leaf only. The Nusselt number *Nu* is the analogous number for heat transfer, enabling direct comparison of heat transfer rates in any fluid (ecologists' interests are usually, but not always, confined to air and water):

$$Nu = \frac{C l}{\rho c_p D_H (T_s - T_a)} \tag{2.5}$$

where *C* is the heat flux density (J m⁻² s⁻¹), ρ is the density of the fluid (kg m⁻³), c_p is the specific heat at constant pressure (J °C⁻¹ kg⁻¹), *D_H* is the molecular diffusion coefficient for heat in the fluid concerned (m² s⁻¹), *T_s* is the surface temperature and *T_a* is the temperature of the bulk of the fluid (°C). A boundary layer resistance for heat transfer from one side of the leaf is calculated as $r'_a = 1/D_H Nu$.

Formulae for laminar boundary layers

To estimate the effect of wind on boundary layer resistance of a flat plate the following formulae are widely used because they can be derived from theoretical considerations and are also a good representation of the large body of experimental data, in the engineering sciences at least:

$$Sh = 0.66 Re^{0.5} \left(\frac{\nu}{D}\right)^{0.33} \tag{2.6}$$

$$Nu = 0.66 Re^{0.5} \left(\frac{\nu}{\kappa}\right)^{0.33} \tag{2.7}$$

where κ is the thermal diffusivity. Derivation of 2.6 and 2.7 can be seen in suitable textbooks such as Welty, Wick & Wilson (1969). These equations imply that the ratio of resistances for different entities are related to each other as

$$\frac{r'_a H_2O}{r'_a heat} = \left(\frac{\kappa}{D_v}\right)^{0.66} = 0.93 \tag{2.8}$$

$$\frac{r'_a CO_2}{r'_a heat} = \left(\frac{\kappa}{D_c}\right)^{0.66} = 1.32 \tag{2.9}$$

$$\frac{r'_a CO_2}{r'_a H_2O} = \left(\frac{D_v}{D_c}\right)^{0.66} = 1.39 \tag{2.10}$$

and not in simple inverse proportion to the respective values of *D* as suggested from first principles (equations 2.1 and 2.2).

Formulae for turbulent boundary layers

As we have seen, boundary layers over leaves are frequently turbulent, or partly turbulent, and so these relationships (equations 2.6-2.10) cannot be expected to apply. Alternative expressions for *fully developed turbulent flow* are available in which the relationship between exchange rate and Reynolds number is steeper than for laminar flow (Bayley, Owen & Turner 1972):

$$Sh = 0.03 Re^{0.8} \left(\frac{\nu}{D}\right)^{0.33} \tag{2.11}$$

$$Nu = 0.03 Re^{0.8} \left(\frac{\nu}{\kappa}\right)^{0.33} \tag{2.12}$$

However, these expressions are valid only at high Reynolds numbers and do not provide reliable estimates when *Re* is less than 2×10^4 , as is often

the case for leaves in the natural wind. Moreover they may not include proper contribution for the laminar sublayer, nor for the buffer zone between this and the turbulent flow, especially for a hairy or rough leaf. Furthermore, we have seen that the boundary layer over a leaf may be laminar near the leading edge and on the flatter parts of the leaf, and turbulent where the air flow is tripped by uneven topography. In view of this complexity we cannot expect good agreement between experimental data and standard relationships, whether laminar or turbulent boundary layer theory is applied.

Experimental data

Experimental data are plotted in Fig. 2.2, along with lines drawn from standard relationships. Most results suggest that exchange rates for leaves are higher than predicted by the equations for laminar boundary layers, often by a factor of two. However, the slope of the relationship is not steep enough to indicate fully developed turbulent flow except at the three highest Reynolds

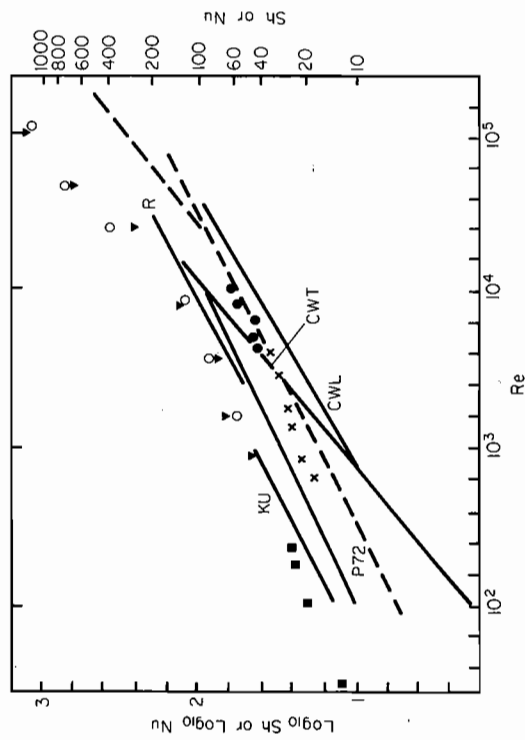


Fig. 2.2. Exchange rates for model leaves. The scatter about the standard relationship, shown by a dashed line, is considerable. Kuiper (KU), Rashke (R) and Slatyer & Bierhuizen (SB), all reproduced from Monteith (1965); Thom (1968) (\times), Parkhurst *et al.* (1968) (\bullet), Pearman *et al.* (1972) (P72), Clark & Wigley (1975) with turbulent (CWL) and laminar (CWL) free streams and Grace & Wilson (1976) with turbulent (\circ) and laminar (\blacktriangledown) free streams.

numbers used by Grace & Wilson (1976). We may conclude that these data and the observations made with a hot-wire anemometer (Fig. 2.1), are consistent with the view that boundary layers over leaves are usually neither laminar nor strictly turbulent, but that a mixed regime prevails.

Estimates of r_a

The effect of wind speed on boundary layer conductance or resistance is shown in Fig. 2.3, on the assumption that the boundary layer is laminar. This graph may be used for estimation purposes, but in view of what has been said it must be realized that the conductance thus obtained may be an underestimate by a factor of two. Caution should also be applied when interconverting resistances for different entities using equations 2.8–2.10: in those parts of the leaf where the boundary layer is turbulent the resistances for different entities will not be as calculated.

A general point is evident from Fig. 2.3. It is that *leaf size* is important in determining the coupling of leaves to the atmosphere; small leaves have

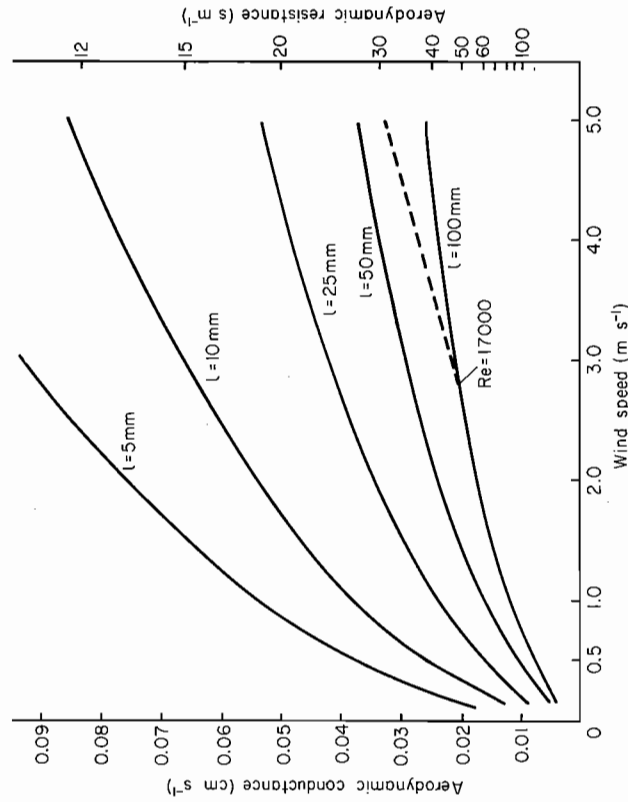


Fig. 2.3. Aerodynamic conductance for leaves of various dimension according to the standard relationships derived from engineering studies. For large leaves at high wind speed (3 m s^{-1}) the calculation for a turbulent boundary layer (broken line) gives a higher conductance than that for a laminar boundary layer (solid lines).

high boundary layer conductances and so are more closely coupled to the atmosphere than large ones.

There is another difficulty in applying Fig. 2.3 for specific estimation purposes. When one leaf is close to another, or close to another object such as a rock protruding from the ground, boundary layers will tend to coalesce.

There have been few studies of this phenomenon despite its ecological importance. In one case, Landsberg & Thom (1971) measured the boundary layer resistance of the bunches of spruce needles which form a shoot, and they found that the boundary layer resistance was twice that calculated from data for an isolated needle.

EFFECT OF WIND SPEED ON r_a OF VEGETATION

A more overall view of the exchange rates between vegetation and atmosphere is obtained if the vegetation is treated as a single rough surface which by virtue of its roughness, slows down the air flow. This results in a much-reduced wind speed immediately above the vegetation—in other words a boundary layer is formed. In this process momentum is transferred from the bulk of the atmosphere (the momentum concentration is ρu) to the leaves and branches in the vegetation. The air just above the vegetation has a reduced momentum and the air in contact with surfaces has no velocity, and hence no momentum at all. The whole process may be regarded as a downward flux of momentum from a source, the atmosphere, to an imaginary sink at height d in the vegetation. As the air over the vegetation is turbulent the basic mechanism involved here is turbulent transport, whereby momentum, heat and gases share the same vehicle of transport—the parcels of air whose motion constitutes the turbulence. It is worthwhile asking the question 'what attributes of the vegetation determine the rate of momentum exchange?' The answer should be found in a comparison of windspeed profiles of different sorts of vegetation.

Many workers have fitted the following equation to measurements of the wind speed made above the vegetation at several heights (z):

$$u(z) = \frac{u_*}{k} \ln \left(\frac{z-d}{z_0} \right) \quad (2.13)$$

where u_* is a parameter called the friction velocity (m s^{-1}), k is von Karman's constant (a pure number), d is the zero plane displacement (the apparent level inside the canopy where the wind speed is zero—the sink for momentum), and z_0 is the roughness length.† For a good discussion of this equation, including a physical interpretation of the parameters, the reader is referred to Thom (1975).

Examples of wind profiles are given in Fig. 2.4a. The profiles start at a higher point above the ground for the tall vegetation because the roughness elements are held aloft. The dotted portions are extrapolated to a virtual

† To simplify this discussion, the meteorological conditions are assumed to be neutral (i.e. with a temperature gradient close to $-0.01^\circ \text{C m}^{-1}$). In unstable conditions, i.e. a gradient of 1°C m^{-1} , turbulent transfer is enhanced by buoyancy. In 'stable' conditions, when temperature decreases with height by -1°C m^{-1} , vertical motion is suppressed.

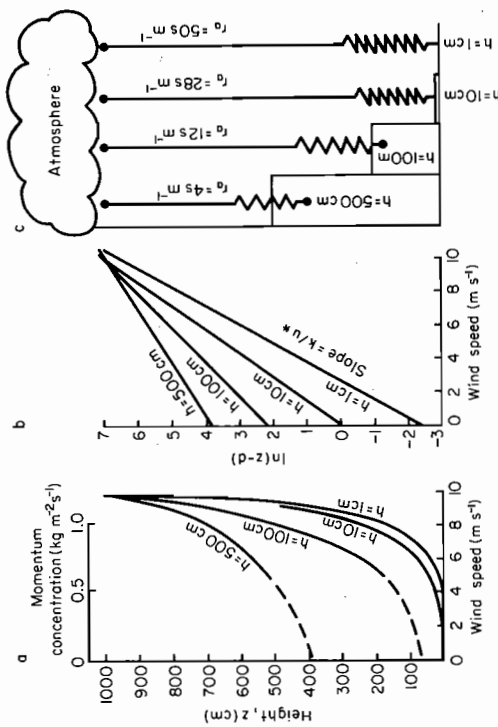


Fig. 2.4. Momentum exchange as affected by vegetation height: (a) vertical profile of momentum over vegetation of four heights, h , when the wind speed at 10 m corresponds to a strong breeze; (b) the logarithmic plot used to obtain the roughness parameter z_0 ; (c) calculated resistances to momentum transfer between 10 m above the ground and the hypothetical momentum sink in the vegetation. The data from which these curves were drawn were calculated using equation 2.13.

point of zero windspeed at d , which is normally between 0.6 to 0.8 of the vegetation height. Also the profiles are a different shape: immediately over short vegetation the wind speed changes very rapidly with height, implying that the mixing process is less effective than over tall vegetation.

The difference between the shapes of the profiles is better shown in Fig. 2.4b, where the ordinate is a logarithmic scale adjusted for differences in zero plane displacement. The slope of these lines, from equation 2.13, can be shown to be k/u_* . The intercept provides the important parameter z_0 , the roughness length, which specifies the ability of the vegetation to capture momentum. Tall vegetation is always rougher than short vegetation, and for most crops $z_0 \approx 0.1h$.

The more gradual change in wind speed with height over the rougher vegetation implies that the air is better mixed: the turbulent transfer coefficient must be high and the momentum resistance r_a^m must be low. Monteith (1973) and Thom (1975) have explored the relationships between z_0 , and r_a^m : an important result is

$$r_a^m = \{ \ln(z-d)/z_0 \}^2 / (k^2 u_*^2) \quad (2.14)$$

This enables a resistance to be found provided that z_0 and d can be estimated. In Fig. 2.4c the resistance has been calculated for each vegetation height on the assumption that $z_0 = 0.1h$ and $d = 0.7h$ —these values seem to be

approximately correct for most agricultural crops and for some wild vegetation. Resistance is very sensitive indeed to vegetation height, being least for the tallest stands (Fig. 2.4c).

Wild vegetation may not conform to the relationship $z_0 = 0.1h$, due to the extreme range of plant spacing, lack of homogeneity (as in tropical rain forest), or canopy smoothing (as in salt-sprayed coastal vegetation). Recently Garratt (1977) has compiled data from a diversity of vegetation types. From his graph it should be possible to select a suitable value of z_0 , and so estimate r_a^m , for any vegetation (Fig. 2.5).

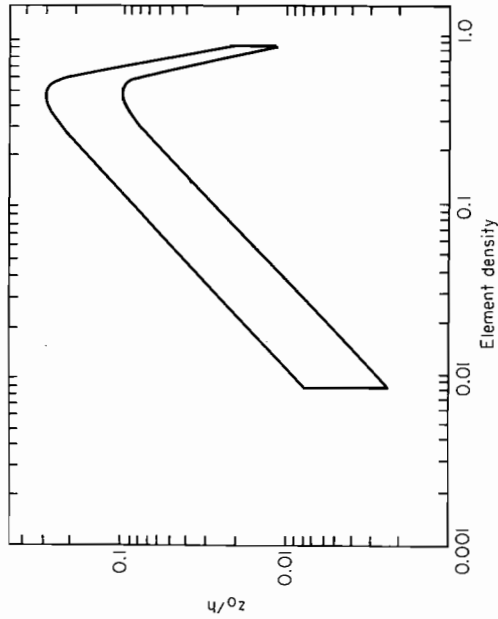


FIG. 2.5. The influence of vegetation density on the fraction z_0/h , where z_0 is the roughness length and h is the plant height. Element density is defined as the plant silhouette area normal to the wind per unit surface area occupied by each plant. Most vegetation falls within the density range 0.05 to 0.15. The envelope contains the scatter of observational data (Garrett 1977).

Equation 2.14 shows that r_a^m is inversely proportional to windspeed, assuming that z_0 and d are insensitive to wind (some effect of wind on z_0 and d is likely as the canopy becomes smoothed or parted with changes in the wind speed). Fig. 2.6 shows the effect of wind on the resistance r_a^m and conductance g_a^m for vegetation of differing heights, again assuming $z_0 = 0.1h$, $d = 0.7h$, and further assuming that z_0 and d are not affected by windspeed.

In the turbulent boundary layer over vegetation, the aerodynamic resistance may be expected to be the same irrespective of the diffusing entity, i.e.

$$r_a^m = r_a^{gas} = r_a^{heat} \quad (2.15)$$

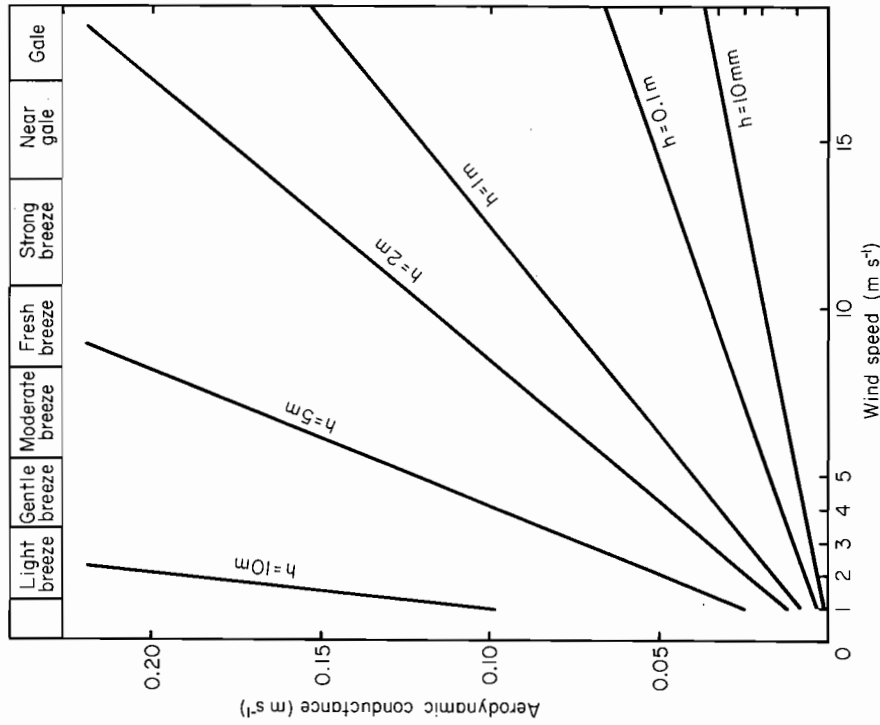


FIG. 2.6. The effect of vegetation height on aerodynamic conductance, calculated from equation 2.11 assuming $z_0 = 0.1h$. The figures on the lines are the heights of the vegetation (m).

In practice, however, the aerodynamic resistance for momentum transfer to the vegetation may differ substantially from the resistances for heat and gases. One reason for this is that the 'sinks' for momentum within the canopy are all the structural elements, living or dead, which slow down the air flow. The 'sources' and 'sinks' for gases and heat exchange may not be the same as this, and will be modified by physiological activity; for carbon dioxide transfer, for instance, only the leaves are active. There is another reason too. When air flows over a leaf surface momentum exchange across the boundary layer occurs by *skin friction*, a process analogous to the diffusion of heat or gas. If on the other hand the surface is held perpendicular to the flow the air is blocked and so very considerable momentum is exchanged, by

form drag, without a corresponding increase in the exchange of heat or gas. The net effect is that the apparent sources and sinks for heat and water vapour occur at lower level in the canopy than the sink for momentum, and so—because of the increased path length—the aerodynamic resistances for them are greater. Monteith (1973, pp. 197–198) and Thom (1975, pp. 90–92) make suggestions about the quantitative relationships between these resistances.

The general point, that tall plants are more closely coupled to the atmosphere, seems important. That there are indeed substantial differences in the microclimate of tall and short vegetation is demonstrated by field observations: Salisbury and Spomer (1974) showed that the temperatures of cushion plants in the alpine environment were several degrees higher than those of nearby 'erect' plants. In further support, it is well known that species of wide geographical distribution are of shorter stature in their most 'exposed' situations, and that this short stature is maintained even when individuals are transplanted to a more mesic site (e.g. Clausen, Keck & Hiesey 1940). Natural selection evidently favours short stature at 'exposed' sites and this may result from the higher temperatures. Similar arguments may be made for coastal vegetation in relation to salt spray; for short plants, weakly coupled to the atmosphere, receipt of salt droplets will be less than for their taller neighbours.

WIND AND TRANSPIRATION

The influence of wind speed on transpiration rate and surface temperature cannot be estimated from a knowledge of r_a alone, because the extent to which its influence is felt depends on other factors, notably the available energy and stomatal conductance. The heat balance equation of a leaf may be stated

$$\mathbf{R} + \lambda\mathbf{E} + \mathbf{G} + \mathbf{C} + \mathbf{S} + \mathbf{P} = 0 \quad (2.16)$$

where \mathbf{R} is the net radiation, $\lambda\mathbf{E}$ is the energy used in evaporating water (λ is the latent heat of vaporization of water), \mathbf{G} is the rate of exchange with the other parts of the system by conduction, \mathbf{C} is the convective heat exchange, \mathbf{S} is the rate of change in stored heat, \mathbf{P} is the rate of conversion of radiant energy to chemical energy by net photosynthesis.

In many cases \mathbf{G} , \mathbf{S} and \mathbf{P} are small compared with \mathbf{R} (e.g. see Cernusca & Seeber, this volume), and so the 'available' energy \mathbf{H} is roughly equal to the net radiation. It is 'available' inasmuch as it may drive evaporation or be converted to sensible heat, warming the leaf.

$$\mathbf{H} = \mathbf{C} + \lambda\mathbf{E} \quad (2.17)$$

The convection of heat from the leaf proceeds at a rate which depends on

the difference in the temperature of the surface and the ambient air ($T_s - T_a$)

$$\mathbf{C} = \frac{\rho c_p (T_s - T_a)}{r_a^{heat}} \quad (2.18)$$

where r_a^{heat} is the boundary layer resistance for heat, and ρ is the density of air.

Similarly the evaporation rate depends on the difference between the saturation vapour pressure for water at the evaporating sites within the leaf ($e_s(T_s)$) and the vapour pressure of the ambient air, e

$$\mathbf{E} = \frac{\rho c_p (e_s(T_s) - e)}{\lambda \gamma (r_s^{H_2O} + r_a^{H_2O})} \quad (2.19)$$

where γ is the psychrometric constant and $r_s^{H_2O}$ is the stomatal resistance.

In a well-watered plant with its stomata open the evaporation rate may be high, using up most of the available energy so that \mathbf{C} is low. If stomata are shut then the evaporation rate is low, and most of the available energy will go towards increasing T_s .

The importance of these equations is that they may be solved to estimate the influence of wind on leaf surface temperatures or on evaporation rates from plant leaves (Linacre 1964; Monteith 1965; Gates & Papian 1971).

When this is done we obtain the somewhat unexpected result that in quite a lot of conditions an increase in the wind causes a *decrease* in the rate of transpiration, not an increase (Fig. 2.7). This is because the wind cools the leaf, and at this lower temperature the concentration of water vapour in water-saturated air is less; consequently the difference between the concentration of water in the sub-stomatal air cavities and that in the bulk of the atmosphere is less. Thus, with a smaller driving gradient, the diffusion rate of water molecules must be correspondingly slower. Yamaoka (1958) demonstrated this experimentally, but his paper has been overlooked until recently (compare Fig. 2.8 with Fig. 2.7).

WIND AND GAS EXCHANGE

The influence of wind speed on \mathbf{F} the maximum rate of uptake of CO_2 may be estimated from a knowledge of r_a and r_s .

$$\mathbf{F} = \frac{\chi_{air} - \chi_i}{r_a + r_s + r_m} \quad (2.20)$$

χ_{air} and χ_i are the concentrations of carbon dioxide in the ambient air and of the sites of photosynthetic carboxylation, respectively; and r_m is the resistance inside the leaf, discussed at length by Jarvis (1971). The value of

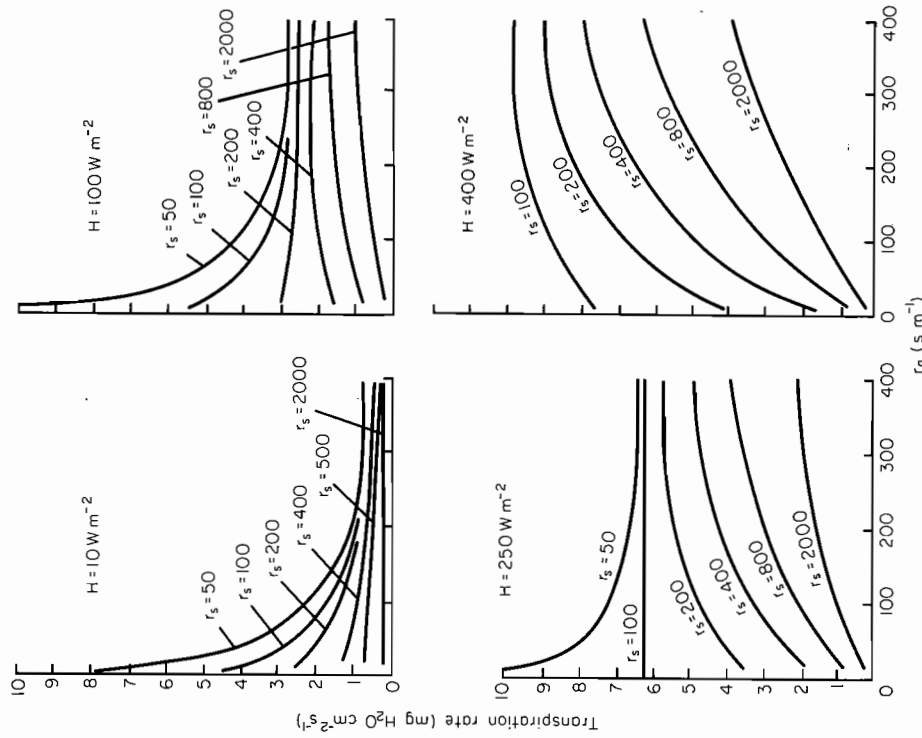


FIG. 2.7. Transpiration rate of leaves as influenced by aerodynamic resistance r_a , stomatal resistance r_s and available energy H . From Grace (1977), calculated from the Penman Monteith equation using an atmosphere saturation vapour deficit of 800 Pa and an air temperature of 15 °C. Units of r_s are sm^{-1} .

χ_i presumably depends on the affinity of the enzyme system for carbon dioxide and cannot be determined directly. Many workers have assumed a value of zero, as an expedient. Since the work of Gaastra (1959) many measurements of r_a , r_s , and r_m have been made; for tabulated examples see Whiteman & Koller (1967), Körner, Scheel & Bauer (1979).

Grace (1977) applied equation 2.20 and inserted various values of aerodynamic resistance to estimate the influence of wind on photosynthesis (using Fig. 2.3). The result suggested that wind had only a small effect on CO_2 exchange, except at extremely low values of wind speed where r_a may

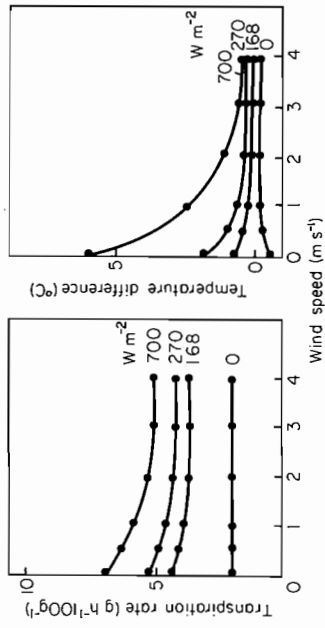


FIG. 2.8. Observed effect of wind speed on the rate of transpiration and leaf temperature in *Cryptomeria japonica*. Air temperature 20 °C, relative humidity 60%. After Yamaoka (1958).

become substantial in relation to $r_s + r_m$. In outdoor conditions it is doubtful whether r_a is often very high as still air rarely occurs—thermal gradients in plant canopies give rise to air movements by natural convection. In the laboratory, rather high values of r_a are apparent in unstirred photosynthesis chambers (Decker 1947; Warren-Wilson & Wadsworth 1958; Avery 1966; Parkinson 1968).

A similar approach to the estimation of the effect of wind speed on gas exchange might be applied to pollutant gases. Each gas is likely to have a somewhat different diffusion path inside the leaf however, so basic research in controlled environment chambers is required to elucidate the value of r_m and its sensitivity to environment and to the physiological conditions of the plant.

The influence of wind on transpiration rate has previously been discussed. The conclusion that wind does not always increase transpiration rate, holds for undamaged leaves. Wind damage to leaf surfaces is often apparent to the naked eye (Bauer 1966; Taylor & Sexton 1972), and Thompson (1974) has demonstrated significant wind damage on a microscopic scale to leaves of *Festuca arundinacea* exposed in a wind tunnel. This damage, resulting from collisions of leaves, involved alterations in the wax depositions on the cuticle and included the rupture of epidermal cells. Such leaves had a much higher conductance to water vapour, both cuticular and stomatal components being affected (Fig. 2.9). Similar abrasion has been reported by MacKerron (1976) in *Fragaria* and by Wilson (1979) in *Acer*, but seems to be negligible in *Picea* (Grace, Malcolm & Bradbury 1975) and *Pinus* (Rees 1979).

The integrity of the cuticle may be much more important than has been previously realized. In drought or in the winter when the ground is frozen, the cuticular resistance to water loss may be critical for the plant's survival. Tranquillini (1976) showed that trees which suffer from 'winter desiccation'

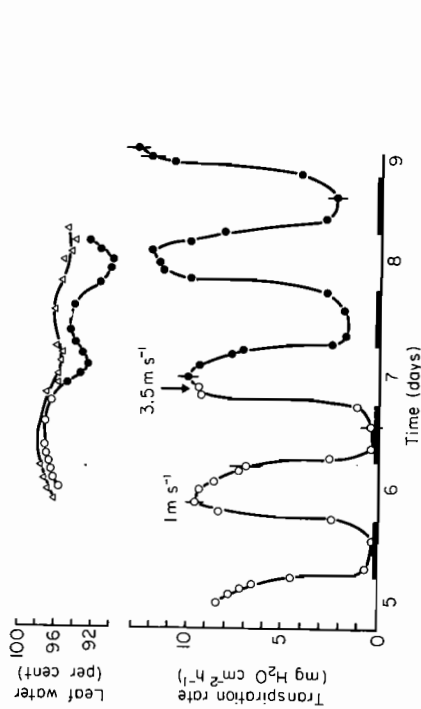


FIG. 2.9. Effect of an increase in the wind speed on the diurnal course of transpiration rate in *Festuca arundinacea* in a wind tunnel. Open symbols denote low wind speed (Grace 1974).

at the tree line do so because in the shortened growing season their cuticle does not fully develop—it remains thinner than in trees from lower altitude and the transpiration rate is consequently higher.

On the other hand, some species are said to shut their stomata in the wind (Martin & Clements 1935; Tranquillini 1969; Caldwell 1970; Davies, Kozłowski & Pereira 1974; Flückiger, Oertli & Flückiger-Keller 1978; Davies, Gill & Halliday 1978). This may be mediated by turgor changes caused by mechanical shock, as suggested to account for the occasional observation that stomata are sensitive to the shock incurred when a porometer cup is attached to the leaf (Knight 1916; Williams 1949; Fenton, Davies & Mansfield 1977).

SOME PHYSIOLOGICAL CONSIDERATIONS

Mechanical stimulus

Several authors have demonstrated that plant growth is sensitive to mechanical stimulus. Neel & Harris (1971) shook *Liquidambar* stems for 30 s daily and observed an 80 per cent reduction of height growth. Moreover these plants became dormant sooner. Rees (1979) describes a series of careful experiments like this on *Pinus contorta* in which the treatments included a continuous shake as well as a brief shake each morning. Although the results were less dramatic than those reported by Neel & Harris (1971), he found that brief shakes were as effective as continuous shaking: height growth and leaf extension were significantly reduced, and he concluded that 'shaking is a potent inhibitor of plant growth'.

How can shaking affect plant growth? The dwarfing effect of wind on plants resembles the effect of drought, and has led authors to think that water stress is the underlying cause of dwarfing, yet we have already seen that wind probably does not increase transpiration rate in most circumstances, and so is unlikely to have an effect on leaf water potential. Moreover, when water potential has been measured in shelter experiments, or in wind tunnel experiments, no cause-and-effect relationship between wind and water stress has usually been found (Russell & Grace 1978, 1979a).

On the other hand, it is well known that *pressure potential* of individual plant cells may change independently of the water potential of the tissue as a whole, as it does in guard cells, where the pressure potential is regulated by the flux of K^+ ions (Penny & Bowling 1974). In some plants, the same mechanism is developed to enable the plant to respond to tactile stimuli; in *Mimosa* and certain other genera the leaves fold up when touched. The cells of the leaf are able to transmit a message to pulvini at the base of each leaflet. When the message is received there is a flux of K^+ ions which in turn results in an osmotic flow of water within the tissue and a change in pressure potential, which causes the leaf to fold (Allen 1969; Findlay & Pállaghy 1978). It is not suggested that such a phenomenon is general to all plants, yet the example shows how pressure potential may be able to respond to a variety of external stimuli.

The importance of pressure potential is that it provides the driving forces for cell expansion (Hsiao *et al.* 1976). Much work on wind or shaking suggests that these treatments prevent the lamina from properly expanding (Martin & Clements 1935; Grace & Russell 1977; Russell & Grace 1978, 1979a). Good measurements of pressure potential on such leaves while they are expanding have not yet been made.

It should be pointed out that other plant responses to tactile stimuli have been reported, including a response in the rate of respiration (Audus 1935; Godwin 1935; Todd, Chadwick & Sing-Dao Tsai 1972), and an increase in the rate of production of the growth substance ethylene (Goeschl, Rappaport & Pratt 1966; Jaffe & Galston 1968).

Displacement from vertical

The action of wind on plants may be construed as a series of displacements of the shoot apex from the vertical. It has been known for a long time by horticulturists that pulling down branches of fruit trees results in the outgrowth of lateral buds which would otherwise have remained dormant. To explain such observations, Wareing & Nasr (1961) suggested that the tree may detect the shoot's orientation in relation to gravity. Longman (1968) measured the growth in length of shoots produced from cuttings of cassava (*Manihot esculenta*) which were inclined at various angles. Although the total

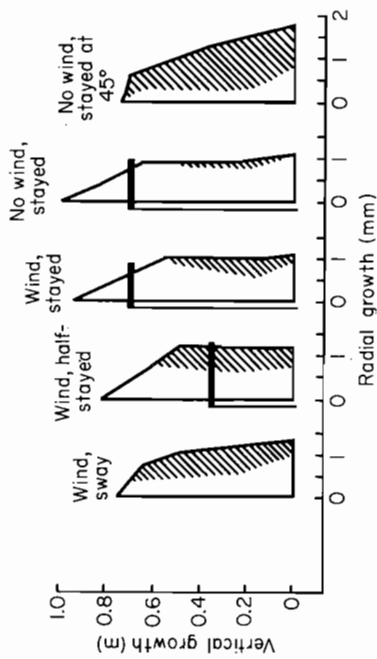


FIG. 2.10. The influence of sway on the height and distribution of wood increment in the stem of *Larix laricina*. Swaying was prevented in some trees by clamping with stays (shown in the diagram as solid bars). Shaded areas denote thick-walled (> 5 μm) tracheids. From Larson (1965).

shoot production was not much affected by angle, the *difference* between shoot growth at the apical end and that at the base was very sensitive to displacement from the vertical; as this displacement increased, the lower shoots outgrew the upper shoots. Such an effect in a mature tree would result in a bushy specimen with reduced leader growth.

The converse is apparently true: Jacobs (1954) supported trees over a period of years so that they could not be displaced from the vertical by the wind. At the end of the experiment they were tall and thin, and unable to support themselves when the stays were removed. A similar experiment on *Larix* by Larson (1965) included a treatment in which the plants were inclined at 45°. Inclined plants developed greater girth than the controls, but increased less in height (Fig. 2.10). He suggested that wind and displacement from the vertical exerted their effect by an influence on the downward gradient of auxin within the plant.

WIND AND STRUCTURAL FAILURE

From a practical point of view the structural failure of crops, caused by wind forces, is of great significance, to both agriculture and forestry (Holtam 1971; Pinthus 1973). An understanding of the principles involved in such wind damage is the essential prerequisite if crops are to be grown reliably in windy places.

The wind forces acting on individual plants that make up the canopy can be established from the within-crop wind profile if the vertical distribution of leaf area is also known (Grace 1977); for a given stratum of canopy

the force acting laterally is $\frac{1}{2}\rho c_d \mu^2 a$ where ρ is the density of air, μ and a are the wind speed and leaf area for that particular stratum and c_d is the drag coefficient for the leaves (a measure of momentum transfer across the boundary layer which must be determined in wind tunnel tests—for example see Thom 1968). This force results in a turning moment about the base of the stem. In addition, an extra turning moment arises when the stem is deflected due to the displacement of the centre of gravity from the vertical. The total turning moment for the plant can then be found by adding the calculated turning moments of all the strata.

Structural failure occurs when the total turning moment exceeds a critical value, when either the stem breaks or the plant is uprooted. This critical value may be found directly by pulling the plants over and measuring the turning moment required. This has been done by Fraser & Gardiner (1967) who found considerable between-site variation in the force required to uproot trees, depending on the soil type and consequent extent of root development.

From a knowledge of the critical turning moment of the plant, together with estimates of wind speeds within the vegetation, it should be possible to predict the threshold wind speed at which structural failure occurs; just as a civil engineer can estimate the critical wind speed for a building design. However, this approach has not been successful: Tani (1963) and Fraser (1964) both found that the wind speed calculated to cause the stem to break was larger than the actual destructive speed. It has been pointed out that plants are aeroelastic structures, in which the fluctuating property of the wind in relation to the natural period of oscillation should be taken into account (just as the suspension bridge of the civil engineer is prone to collapse at rather low windspeeds if the gust frequency happens to coincide with a natural period of swing).

Japanese workers have studied the phenomenon of waving plants (known as 'Honami'), although mainly from a theoretical point of view (e.g. Inoue 1955). At an observational level, Maitani (1979) reported the motions of wheat and *Juncus* plants, recorded with a cine camera, and tried to relate them to the statistics of wind turbulence obtained using a sonic anemometer near the top of the canopy. Displacements of the ear of wheat showed a natural period of oscillation of 0.8 or 0.9 s whilst those of *Juncus* were more variable according to the fluctuations in wind velocity. There was similarity between the power spectrum for wheat deflections and that of wind velocity, both showing a peak around 0.8 Hz—suggesting that eddies of this particular frequency were exciting the wheat ears. Similarity between power spectra in *Juncus* was not clear cut. Differences in the behaviour of the two species may be related to the aerodynamic differences between them: the inflorescence of each wheat plant may act as an efficient momentum-absorber, free to oscillate in simple harmonic motion at the end of an elastic member (the

stem), whilst the tapering *Juncus* leaf may exhibit more complex modes of motion. The study underlines the difficulties in quantitatively understanding the aeroelastic behaviour of plants.

CONCLUSIONS

The application of physical principles to the study of exchange processes between plants and the atmosphere has been remarkably fruitful in advancing our understanding of the influence of wind upon vegetation. These conclusions may be drawn:

1. The boundary layer resistance r_a may be calculated from the wind speed and leaf dimension, although considerable divergence is evident when experimental observations are compared with the calculated values. This divergence may be due to irregularities in the topography of the leaf and turbulence in the air flow, both of which promote turbulence in the boundary layer over the leaf and so may reduce r_a .
2. From a knowledge of boundary layer resistance, the influence of wind on the exchange of gases and other entities between the leaf and the atmosphere may be investigated. The effect of wind on CO_2 exchange is normally rather small, because the boundary layer turns out to be only a small part of the total diffusion pathway. Application of the Penman-Monteith equation to investigate transpiration shows that the effect of wind on water loss is often small, and can be positive or negative. Exceptions to this occur in those leaves prone to surface damage, in which transpiration may be considerably increased by wind action; this seems to occur in grasses and broad-leaved trees but not in conifers. Such surface damage may also affect stomatal behaviour, so the influence of wind on transpiration may be very complex.
3. At a gross level, the micrometeorological approach provides a means of finding the boundary layer resistance over the vegetation. It can be shown that short vegetation is characterized by a high resistance over the vegetation. It is suggested how this may explain the apparent Darwinian fitness of prostrate life forms in cold and windy places; dwarf life forms by virtue of their high boundary layer resistance have the advantage of higher surface temperatures when net radiation is positive.
4. Recent studies suggest that shaking can be a potent inhibitor of plant growth. The mechanism of this effect is not yet known.
5. Catastrophic failure of plant structure as in windthrow of forest trees cannot be predicted from the force calculated from average wind speeds. It is suggested that a plant can be regarded as an aeroelastic structure which becomes excited when the gust frequency coincides with one of its natural modes of oscillation.
6. The term 'exposure' used by ecologists and foresters to describe the

stresses which plants experience in windy habitats cannot be concisely defined, although it may be understood as a close coupling of plant parts to the atmosphere, and may be analysed quantitatively in terms of diffusion resistances. A plant closely coupled to the atmosphere will experience (a) surface temperatures which are not much higher than the temperatures of the surrounding air; (b) fast deposition of any aerosols in the atmosphere such as salt spray; (c) considerable absorption of momentum which may cause structural damage or microscopic damage to the epidermis.

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3. THE SIZE AND SIGNIFICANCE OF DIFFERENCES IN THE RADIATION BALANCE OF PLANTS AND PLANT COMMUNITIES*

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SUMMARY

Measurements made during the last 25 years are presented which suggest that a marked similarity exists in the radiative properties of the leaves and stands of different plant species, especially agricultural ones. The ecological significance of the small differences that have been reported, and their exploitation, both by plants and by man, are discussed.

INTRODUCTION

Several excellent reviews dealing with the radiation balance of plant communities have been published during the last 25 years. A comparison of Sauberer and Hartel's book on the subject published in 1959 (Sauberer & Hartel 1959) with Ross's comprehensive review of radiative transfer in plant communities published in 1975 (Ross 1975) shows the considerable progress achieved during the intervening period in describing the interaction between radiation and plants in physical-mathematical terms.

Despite this progress, there remain many aspects of the subject which cannot yet be treated in this same rigorous fashion and yet are of considerable importance and interest to ecologists. One of these aspects—the size, significance and possible exploitation of differences that have been observed between the radiation balance of different plant species and plant communities—is the subject of this contribution.

METHODS OF MEASUREMENT

Awareness of the exaggeration of the differences in plants' radiative characteristics resulting from the bias inherent in human vision developed slowly

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