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The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field

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Attempts to correlate values of stomatal conductance and leaf water potential with particular environmental variables in the field are generally of only limited success because they are simultaneously affected by a number of environmental variables. For example, correlations between leaf water potential and either flux of radiant energy or vapour pressure deficit show a diurnal hysteresis which leads to a scatter diagram if many values are plotted. However, a simple model may be adequate to relate leaf water potential to the flow of water through the plant.

The stomatal conductance of illuminated leaves is a function of current levels of temperature, vapour pressure deficit, leaf water potential (really turgor pressure) and ambient CO_2 concentration. Consequently, when plotted against any one of these variables a scatter diagram results. Physiological knowledge of stomatal functioning is not adequate to provide a mechanistic model linking stomatal conductance to all these variables. None the less, the parameters describing the relationships with the variables can be conveniently estimated from field data by a technique of non-linear least squares, for predictive purposes and to describe variations in response from season to season and plant to plant.

1. Introduction

The development of the diffusion porometer and the pressure chamber has enabled large numbers of measurements of stomatal conductance (k_s) and xylem pressure potential (Ψ_x) to be made in the field, in recent years. Because the measurements are easily made, very many values have been obtained simply to describe stomatal behaviour and water status in plants. Convenient methods are required to reduce these measurements to manageable proportions and to obtain useful information about plant properties from them. One approach which has been tried is to relate the measurements empirically to the environmental variables using simple (e.g. Millar, Jensen, Bauer & Norum 1971) or multiple (e.g. Smart & Barrs 1973) regression techniques. However, as a general rule it would seem more promising to try to use mechanistic models, the parameters of which would contribute useful information about properties of the plants.

In addition, values of Ψ_x and k_s are sometimes used as aids in the interpretation of concurrent variations in the rates of photosynthesis and evaporation by leaves or canopies, or as inputs to models to predict photosynthesis and evaporation by leaves or canopies, in particular seasons and weather conditions (see, for example, Monteith 1965, Acock, Thornley & Warren Wilson 1971, Reed, Hammerly, Dinger & Jarvis 1976). For these purposes, values of k_s and Ψ_x may be obtained from measurement on the foliage at the time for which the values are needed. However, measurement of both of these plant variables in the field is laborious, if made by intermittent sampling with porometer and pressure chamber, or requires careful maintenance of

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complex apparatus, if made continuously with assimilation chamber and psychrometer. Furthermore, measurement of k_s by diffusion porometer can be made only when the foliage is dry, and long-term enclosure may lead to changes in the physiological properties of the leaves. Consequently, measurements of Ψ_x and k_s in the field are usually made intensively over selected periods of a few hours or days as shown in figures 1 and 2.

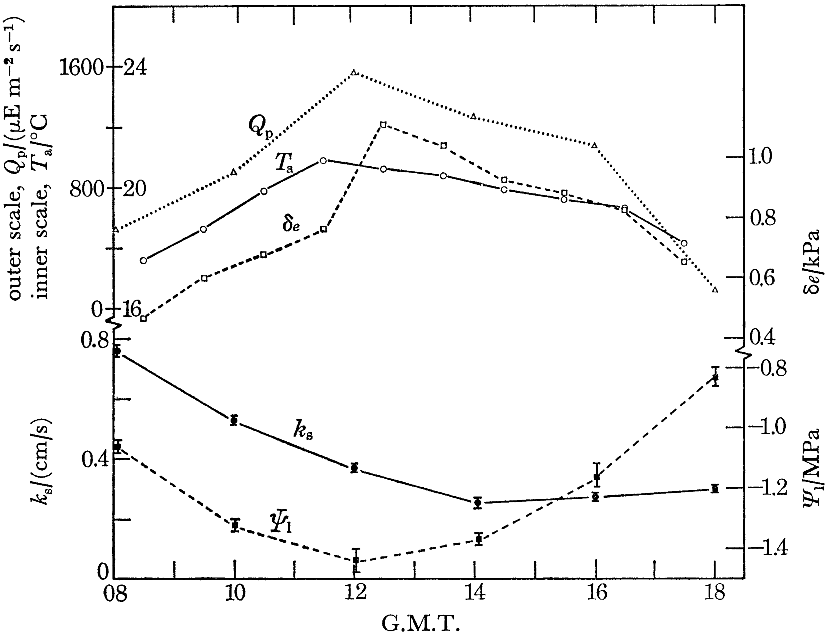


FIGURE 1. Diurnal variation in stomatal conductance (k_s), measured with a diffusion porometer, and leaf water potential (Ψ_l), measured with a pressure chamber, of current year's shoots of Sitka spruce (*Picea sitchensis*) in the upper part of a forest canopy of 25 year old trees on 15 August 1973. Each point is the mean of five measurements; two standard errors of the mean are shown. Concurrent variations in photon flux density (Q_p), air temperature (T_a) and vapour pressure difference (δe) are shown. Data from Watts, Neilson & Jarvis (1976).

Measurements of this frequency provide a considerable amount of detailed information over short periods. However, a similar amount of information is needed throughout the year for the interpretation of measurements of photosynthesis and evaporation, or for the calculation of rates of photosynthesis and evaporation from weather and plant variables. An alternative to very frequent measurement of k_s and Ψ_x in the field is to predict them from measurements of the weather and certain simple plant variables using models containing the parameters derived from occasional periods of measurement in the field. This paper describes two simple models for these purposes.

2. Leaf water potential

The leaf water potential (Ψ_l) is the driving force for the movement of liquid water through the plant. Consequently, the values of Ψ_l attained in the field should be interpreted in relation to the volume flux of water through the plant and the characteristics of the pathway of water transfer from soil to leaf.

The average water potential of the leaf mesophyll (Ψ_l) is nearly identical with the xylem pressure potential in many species, because the solute concentration of the xylem water is low in the extremities of the plant, and equilibration of water potential between leaf mesophyll cells and the xylem is rapid. In this paper, the two will be considered as synonymous.

The pathway of water movement through the plant is a hydraulic system containing frictional resistances to the flow of water. These frictional resistances occur at the internal surfaces of the vessels and tracheids, in simple and bordered pits, in cell walls, in membranes and in the symplasm. The movement of liquid water along a series of frictional resistances requires a difference in potential and this difference is largest when the flow is largest and where the resistance is highest. It is often said that the water deficits in leaves, or the reduction in Ψ_l, occur because the loss of water in transpiration exceeds absorption by the roots. It is, of course, true that the water balance of a cell can change only if the influxes and effluxes of water are unequal. However, to suppose that low water potentials occur in leaves because transpiration from the leaves exceeds absorption by the roots is to obscure the essential nature of water movement through the plant. Under conditions of *steady-state* transpiration from a plant, when absorption of water by the roots equals losses from the leaves, a potential difference must exist between leaves and soil to move water through the frictional resistances. This difference in potential will be larger when transpiration is higher, if the resistances to flow are constant. Water deficits arise because the water potential of cells adjacent to the flow pathway tends to equilibrate with that in the pathway by the movement of water out of the cells. The size of the water deficit depends upon the moisture characteristic of the cells, the resistance to movement of water out of the cells and the water potential in the flow pathway.

For an inelastic, hydraulic system with frictional resistance to flow but no capacitance, a simple one dimensional model of leaf water potential is

$$\Psi_l = \Psi_s - \Sigma q_i R_i - h\rho g, \tag{1}$$

where the subscripts l and s indicate leaf and soil, respectively, and q_i and R_i are the partial, series-linked flows and resistances in the pathway traversed by a molecule of water from soil to leaf (Richter 1973); h is the height above the reference level, ρ the density of water and g the acceleration due to gravity. This model suggests that there should be a unique relation between Ψ_l and the rate of flow of water through the plant for a plant with particular flow path characteristics, provided that the resistance to flow remains constant.

The partial flows in a branched system are not easily measured, whereas the rate of evaporation of water (E) from whole plants in the field may be derived from measurements of the components of the leaf or canopy energy balance. Consequently, (ER_p) is sometimes substituted for ($\Sigma q_i R_i$) in equation (1) as an approximation, namely:

$$\Psi_l = \Psi_s - ER_p - h\rho g. \tag{2}$$

R_p is an effective resistance for the entire pathway of parallel and series-linked conduits between the source of water in the soil and the leaves; it depends strongly upon the development and branching of the vascular tissue into a system of parallel-linked conduits (Jarvis 1975). Investigation of the relationship between Ψ_l and the rate of evaporation of water from the leaves should be informative about the properties of this pathway. In addition, the dependence of Ψ_l on evaporation rate should provide a means for rationalizing the apparent effects of many environmental variables on Ψ_l, and provide a means for the prediction of Ψ_l from a knowledge of the environmental conditions.

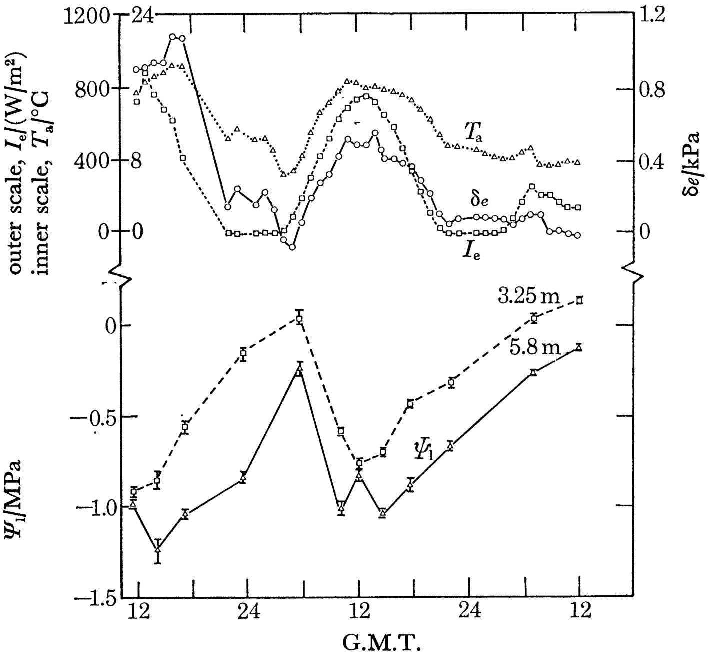


FIGURE 2. Diurnal variation in leaf water potential (Ψ_l) at two heights above the ground in a forest canopy, as in figure 1 (2–4 June 1970). Concurrent variations in irradiance (I_e), T_a and δe are shown. (Redrawn from Hellkvist, Richards & Jarvis 1974, Figure 5.)

Many observations have shown that Ψ_l falls from a high value in the morning to a low value in the middle of the day and then rises again in the afternoon as shown in figure 2 (Klepper 1968, Carr 1971, Goode & Higgs 1973, Jackson 1974). The value of Ψ_l appears to follow air temperature (T_a), vapour pressure deficit (δe) and irradiance (I_e). For example, simple linear regressions of Ψ_l on δe or I_e have been found to account for 70 to 95 % of the variation in Ψ_l over short periods of time (Millar, Jensen, Bauer & Norum 1971; Smart & Barrs 1973).

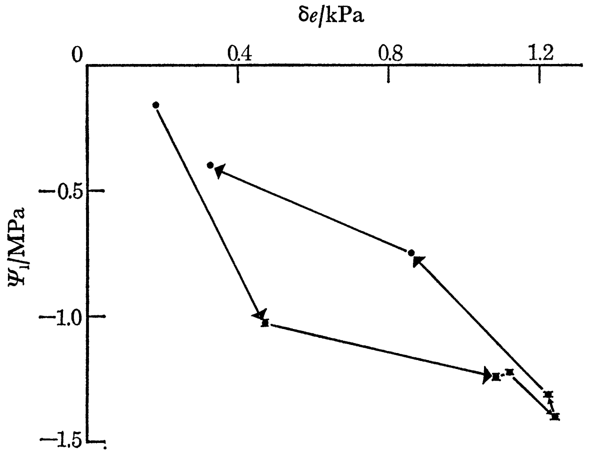


FIGURE 3. The relation between the water potential (Ψ_l) of leaves on hedgerow apple trees (Cox's orange pippin; 26 July 1973) and the vapour pressure difference (δe) during the course of a day. The arrows mark the course of time from dawn to dusk. Each point is the mean of five measurements. Two standard errors of the mean are indicated when they are larger than the symbol. (Redrawn from Landsberg *et al.* 1975, Figure 5.)

However, plots of the diurnal values of Ψ_l against δe (figure 3) or available energy (A) (figure 4) usually show marked hysteresis. This hysteresis results from the simultaneous dependence of Ψ_l on both δe and A. When both increase and decrease in phase together, little or no hysteresis occurs but when the changes in δe lag behind the changes in A, as usually occurs, marked hysteresis results. This hysteresis can introduce appreciable variation into simple regressions of Ψ_l on δe. Multiple regression analysis allows for this with the result that the variation in T, δe and I_e may account for up to 96% of the variation in Ψ_l (Smart & Barrs 1973). However, it would seem more promising to attempt to interpret Ψ_l as a function of these environmental driving variables in terms of their effects on the flow of water through the plant as specified by equation (2).

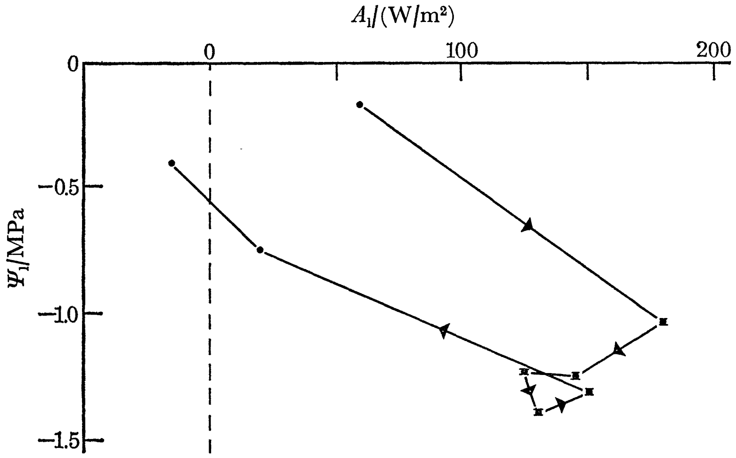


FIGURE 4. The relation between the water potential (Ψ_l) of leaves on hedgerow apple trees and the available energy (A_l) during the course of a day, as in figure 3. A_l is the net radiation absorbed per unit leaf area. (Redrawn from Landsberg *et al.* 1975, Figure 6.)

The Monteith (1965) modification of the Penman equation shows that E is not linearly dependent on any one environmental variable but that:

$$E = \frac{sA + c_p \rho \delta e k_a}{\lambda(s + \gamma(1 + k_a/k_s))}. \tag{3}$$

The rate of evaporation per unit area is a strong function of both A and δe and a weaker function of windspeed, through its effect on the boundary layer conductance (k_a), and of air temperature, through its effect on s (the slope of the relation between saturation vapour pressure and temperature). λ, c_p, ρ and γ are the latent heat of vaporization of water, the specific heat of air at constant pressure, the density of air and the psychrometric constant, respectively; they are all weak functions of temperature. E also strongly depends on the stomatal conductance (k_s) and consequently is affected by all the environmental and physiological variables which affect k_s (see §3).

Consequently it is not to be expected that Ψ_l will be a simple linear function of A, δe or T. However, the same values of Ψ_l plotted in figures 3 and 4 do show a close linear relation with evaporation rate (figure 5). In a similar treatment to that used here, Elfving, Kaufmann & Hall (1972) obtained curvilinear relations. However, they neglected the energy term in the evaporation equation, assuming that E was given by $(\delta e\, k_a)/(1 + k_a/k_s)$. From equation (2), the slope of the line in figure 5 gives the effective resistance of the pathway to water transfer,

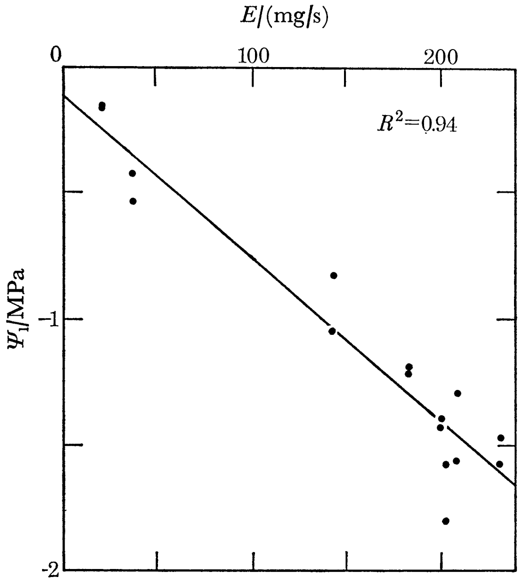
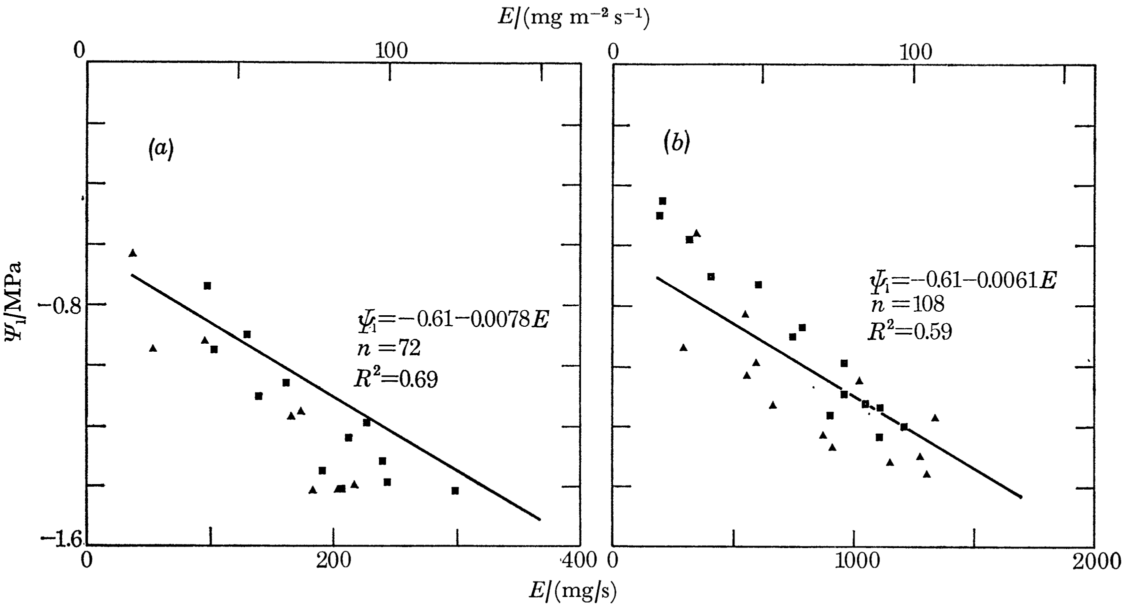


FIGURE 5. The relation between leaf water potential (Ψ_l) of leaves on hedgerow apple trees and the rate of evaporation per tree (E). E was calculated from the energy balance of the leaves by using equation (3) and measured values of A, k_s, k_a, δe and air temperature, and the leaf area per tree. (Redrawn from Landsberg *et al.* 1975, Figure 7.)



FIGURES 6*a* AND *b*. The relation between leaf water potential (Ψ_l) and evaporation rate (E) from (*a*) a 25 year old stand of Sitka spruce at Fetteresso forest (June–September 1973, 4100 trees/ha, leaf area index *ca.* 10) and (*b*) a 43 year old stand of Scots pine at Thetford forest (June 1973, 800 trees/ha, leaf area index *ca.* 4.3). The points are from measurements made on two separate days at each site. The regression lines have been calculated from 8 and 9 days measurements, respectively. Each point is based on five measurements of Ψ_l, the standard error of which was less than 0.05 MPa. E was measured by the Bowen ratio method by (*a*) P. G. Jarvis, G. B. James & B. Davidson and (*b*) Gash & Stewart (1975) respectively. The measurements of Ψ_l were made by (*a*) W. R. Watts & R. E. Neilson and (*b*) J. M. Roberts, respectively.

and the intercept on the ordinate gives an effective source water potential. Figures 6*a* and *b* show similar relations between Ψ_1 and E for Sitka spruce (*Picea sitchensis*) and for Scots pine (*Pinus sylvestris*) on two different days, and regression lines based on measurements over eight or nine days. The ranges of the evaporation rates (expressed per unit ground area) and of the water potentials, and the parameters of the regression lines, are similar at the two sites. It should be emphasized that the spruce and pine data were collected completely independently by different groups of people at sites *ca.* 800 km apart. I am greatly indebted to Dr J. M. Roberts and Mr J. B. Stewart of the Institute of Hydrology for the provision of the Scots pine data.

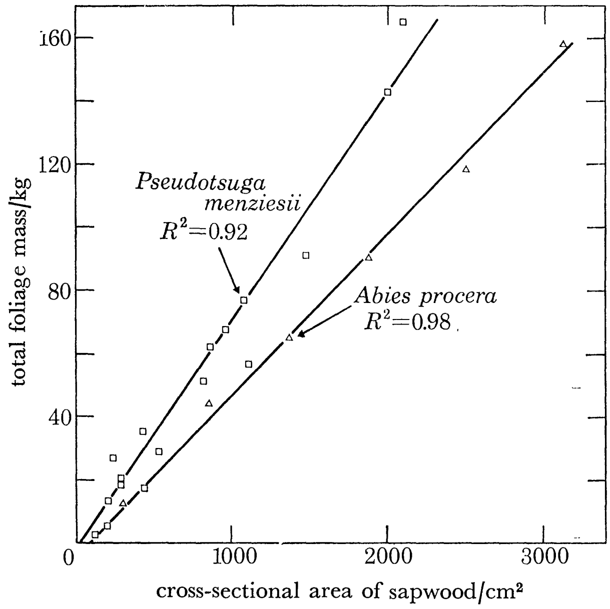


FIGURE 7. The relation between the mass of foliage on a tree and the cross-sectional area of the sapwood at breast height for Douglas fir and noble fir trees of a range of sizes. (Redrawn from Grier & Waring 1975, Figure 1.)

At the Fetteresso Forest site, there were approximately 4100 stems/ha (hectare), whereas at Thetford there were approximately 800 stems/ha. Thus at equal evaporation rates per unit ground area, there was five times as large a volume flow through the Scots pine trees as through the Sitka spruce trees, for approximately the same drop in water potential. Thus the resistance to flow in the pine trees was only about one fifth of the resistance to flow in the spruce trees. This difference occurred despite the fact that the pine trees (top height of *ca.* 15.5 m) were approximately 4 m taller than the spruce trees (top height of *ca.* 11.5 m). As a possible explanation, I suggest that the lower flow resistance of the pine trees may result from a larger cross-sectional area of conducting sapwood than in the spruce trees. This might possibly be a species difference: *Pinus ponderosa*, for example, has a much larger sapwood cross-sectional area than several species of spruce or fir (Lassen & Okkonen 1969). However, it may equally well be the result of homeostasis in the development of sapwood by the trees. It is most unlikely that the spruce trees, after thinning to the same area density as the pines, will have much lower Ψ_1 as a result of the higher rates of evaporation per tree. Instead, R_p will almost certainly fall, as a result of the growth of additional sapwood cross-sectional area in the stem and branches, concurrent with an increase in the amount of leaves in the canopy, as found by Grier & Waring

1975 (figure 7). This should result in the maintenance of Ψ_l within approximately the same limits (Jarvis 1975, figure 8).

Hysteresis is also evident sometimes in the relation between Ψ_l and E (figure 8) because Ψ_l shows a tendency to peak later in the day than E. This might result from differential errors in the determination of E in the morning and afternoon, because of differences in the size of the gradients of temperature and humidity. Alternatively, there may be a real change in the flow resistance of the tree during the course of the day, higher resistances to flow occurring in the afternoon than in the morning. This could result from the fall in water potential during the day causing contraction in the diameter of the tracheids and displacement of the torus in the bordered pits (see Gregory & Petty 1973). Another plausible explanation is that the hysteresis is caused by a shift downwards in the sources of available stored water in the plant itself during the day (Jarvis 1975). When transpiration begins, water will tend to be withdrawn simultaneously from all sources in the plant and soil because of the hydraulic nature of the pathway.

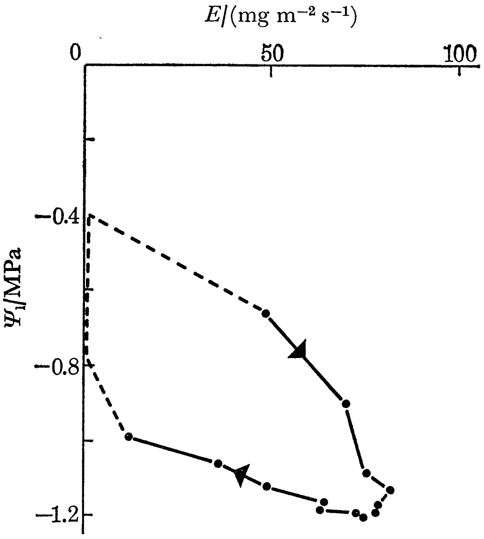


FIGURE 8. An extreme example of hysteresis in the relation between leaf water potential (Ψ_l) and evaporation rate (E) for Scots pine at Thetford Forest. Details as in figure 6*b*. (Data provided by J. B. Stewart & J. M Roberts.)

Initially it is to be expected that most water will move to the liquid-air interface in the leaf from the nearest sources of most readily available water, such as the cells in the leaves, branches and sapwood in the tree crown region. Since these cells are sources of water of finite volume, their capacity to supply water decreases as it is withdrawn and as their water potential tends towards that of the xylem. Consequently a front of water potential and water deficit spreads down through the plant appearing at lower levels somewhat attenuated and with a phase shift. In small herbaceous plants with little storage capacity, both the attenuation and the phase shift may be negligible, but in the stems of trees they are considerable (figure 9). In the afternoon all water transpired must either be withdrawn from storage in the lower levels of the plant or from the soil. Consequently, lower leaf water potentials are likely to be required to maintain a particular transpiration rate than in the morning.

While the explanations suggested above are conjectural, it is apparent that analysis of the values of Ψ_l in those terms provides stimulation for investigation of additional properties of the trees of a more causal nature. For example, it becomes important to know the storage capacity of different tissues in different parts of the plant and the amounts of water coming out of the various stores during the course of the day. More needs to be known about the role of the sapwood as a conducting and storage tissue and possible homeostasis in the cross-sectional area of the sapwood consequent upon changes in the area density of trees. In addition, the model adequately summarizes the interacting effects of radiation, temperature and vapour pressure deficit on Ψ_l; it enables the reduction and interpretation of field measurements of Ψ_l; and it may also be useful in the prediction of stomatal conductance (see §3) or evaporation rate.

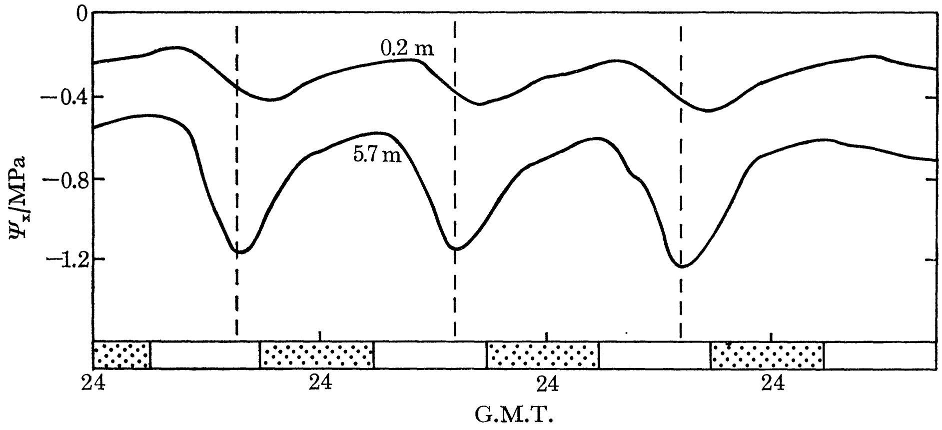


FIGURE 9. Diurnal variation in the xylem pressure potential (Ψ_x) at just above the ground and at the base of the crown in a Sitka spruce tree at Fetteresso Forest during three sunny days (18–21 August 1971). (Redrawn from Richards 1973, Figure 3.5.)

3. STOMATAL CONDUCTANCE

The conductance of illuminated stomata depends upon the current level and history of several environmental variables (Meidner & Mansfield 1968; Neilson & Jarvis 1975). A satisfactory conceptual model to include the known effects of the environmental variables upon k_s depends upon an adequate knowledge of the mechanism of stomatal action at the cellular level. Unfortunately, at the present time the mechanism is not understood in sufficient detail to enable us to specify each partial process and how it is affected by the environmental variables. Consequently, it is not yet possible to interpret the effects of environmental variables on k_s with a mechanistic model of stomatal action.

Nonetheless, a phenomenological model to predict k_s can be made from experimentally determined relations between k_s and the environmental variables. The general form of these relations has been established. The parameters in the relations depend upon the physiological condition of the plants, the previous weather and the season. Consequently, they must be determined at intervals to establish their seasonal course so as to enable calculation of the rate of evaporation and photosynthesis throughout the year. The seasonal variation in the parameters describes the changing adaptation of k_s to the environment. The model described here was developed in close collaboration with Dr K. L. Reed, Department of Natural Resources, Olympia, Washington, U.S.A. A more complete presentation of the model will be made elsewhere.

The variables

The steady state stomatal aperture or conductance depends on photochemical processes and is a function of the quantum flux density (Meidner & Mansfield 1968). The k_s of illuminated stomata is also a function of ambient CO_2 concentration (Meidner & Mansfield 1968), leaf-air vapour pressure difference (Lange, Lösch, Schulze & Kappen 1971), leaf temperature (Neilson & Jarvis 1975) and leaf water status (Stålfelt 1955). We shall restrict attention to these five variables although leaf temperature and leaf water status also depend on several additional environmental variables which influence the leaf energy balance and supply of water to the leaves.

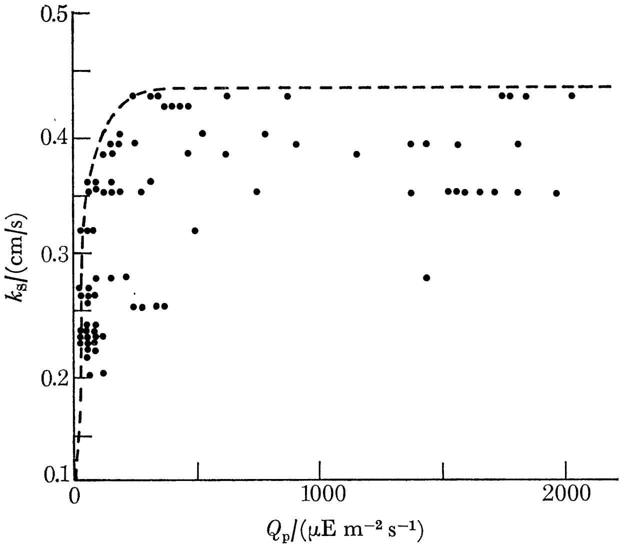


FIGURE 10. A scatter diagram of measurements of stomatal conductance (k_s) of current years shoots of Sitka spruce, in the upper part of the canopy at Fetteresso Forest, plotted against the photon flux density (Q_p) at the time of measurement (Spring, 1973). The dashed line indicates the probable upper limit of the observations. (Data from Watts, Neilson & Jarvis 1976.)

Leaf water potential has been taken as an indication of water status because values are readily available, although it is by no means the most relevant water status variable (see, for example, Turner 1974). Since k_s depends on these five major variables, field measurements of k_s do not usually show a clear relationship with any one of the variables. On many occasions k_s is reduced below the value expected, at a particular value of the independent variable, as the result of the influence of one or more of the other variables. This results in a scatter diagram when k_s is plotted as a function of any one independent variable (figures 10 and 11). Provided that enough measurements have been made adequately to cover the variable space, the upper limit of the scatter diagram indicates the response to the particular independent variable, when the other variables are not limiting. However, this objective is rarely achieved in the field and the upper limit is usually discontinuous and irregular. Consequently, the form of the functional relations between k_s and each driving variable is best determined in controlled environments. Once the form of the relations is known, the parameters in the relations can be determined from a suitable body of field data by using non-linear least squares (e.g. Reed *et al.* 1976). With these parameters, k_s can then be estimated from the weather on other occasions.

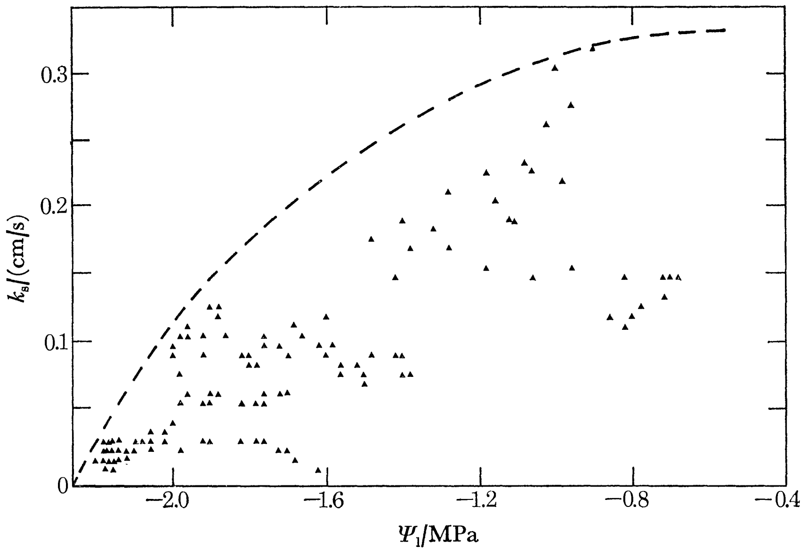


FIGURE 11. A scatter diagram of measurements of stomatal conductance (k_s) of current years shoots of Douglas fir, in the middle of the canopy at the Cedar River Forest site, plotted against the leaf water potential (Ψ_l) at the time of measurement (Autumn, 1973). The dashed line indicates the probable upper limit of the observations. (Data from Leverenz 1974.)

The functions

The observed relation between k_s and photon flux density, Q_p, is similar in form to the relation between CO_2 influx and Q_p and can be approximated by a similar hyperbola (e.g. Turner 1973), with the difference that k_s may have a finite positive value in the dark (figure 12):

$$k_s(Q_p) = b_1 b_2 (Q_p - q)/\{b_1 + b_2(Q_p - q)\}, \tag{4}$$

where $q = b_{10}/b_1$. b_1 is the asymtotic value of k_s at infinite Q_p and b_2 is dk_s/dQ_p at $Q_p = 0$. b_{10} is the value of k_s in the dark and is given by the intercept on the ordinate. b_{10} is introduced to allow for the stomata being open at night, and is not intended to be a cuticular conductance. We have assumed in the following equations that when the stomata are closed the leaf conductance is zero because field data are generally inadequate to define a cuticular conductance.

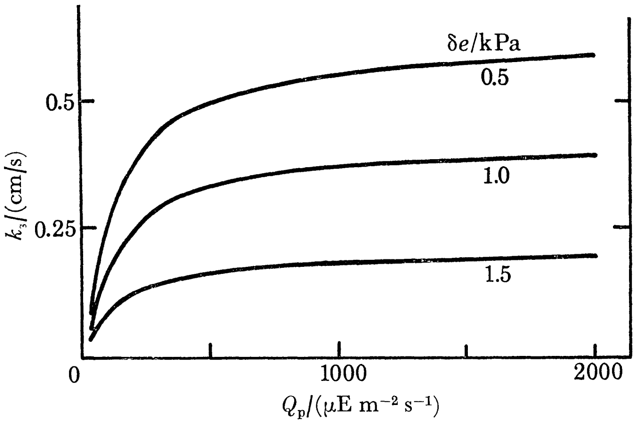


FIGURE 12. The relation between stomatal conductance (k_s) and photon flux density (Q_p), at three levels of vapour pressure difference (δe) as given by equations (4) and (9). Other conditions assumed: $T_a = 10$ °C; $\Psi_l = -0.5$ MPa; $C_a = 300$ cm^3/m^3.

The dependence of k_s on leaf temperature (Sharpe 1973, Neilson & Jarvis 1975) can be represented by the following function (figure 13):

$$k_s(T) = b_3(T-T_l)\,(T_h-T)^{b_4} \quad (0 \leqslant k_s(T) \leqslant 1), \tag{5}$$

where
$$b_3 = 1/(T_0-T_l)\,(T_h-T_0)^{b_4}$$

and
$$b_4 = (T_h-T_0)/(T_h-T_l).$$

$k_s(T)$ is a dimensionless conductance varying between a value of 1 at T_0 and zero at T_l and T_h, the low and high leaf temperatures respectively, at which the curve meets the abscissa.

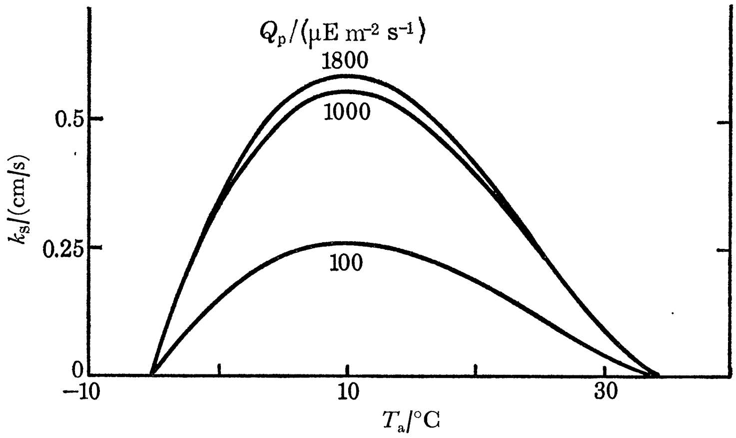


FIGURE 13. The relation between stomatal conductance (k_s) and air temperature (T_a) at three levels of photon flux density (Q_p) as given by equations (5) and (9). Other conditions assumed: δe = 0.5 kPa; Ψ_l = 0.5 MPa; C_a = 300 cm³/m³.

A linear reduction in k_s with increasing vapour pressure difference is assumed (Lange, Lösch, Schulze & Kappen 1971, Schulze *et al.* 1973, Camacho, Hall & Kaufmann 1974, Watts, Neilson & Jarvis 1976, Neilson & Jarvis 1975):

$$k_s\,(\delta e) = 1-b_5\delta e \quad (0 \leqslant k_s\,(\delta e) \leqslant 1), \tag{6}$$

where b_5 is the slope of the relation.

The observed responses of k_s to decreasing Ψ_l include linear proportionality, two sloping straight lines, a threshold region followed by a sloping linear decline, and a continuous curvilinear decline (see, for example, Kanemasu & Tanner 1969, Hansen 1971, Biscoe 1972, Beadle *et al.* 1973, Turner 1974). All of these responses can be more or less approximated by a negative exponential relation (figure 14):

$$k_s\,(\Psi_l) = 1-e^{-b_6\delta\Psi} \quad (0 \leqslant k_s\,(\Psi_l) \leqslant 1), \tag{7}$$

where $\delta\Psi = \Psi_l - \Psi_m$ and Ψ_m is the value of Ψ_l at which the relation extrapolates to $k_s = 0$.

The response of k_s to ambient CO₂ concentration (C_a) (Meidner & Mansfield 1968) is assumed to consist of a threshold region between 0 to 100 cm³/m³ followed by a linear decline to a minimal value at 1000 cm³/m³ (figure 15):

$$k_s(C_a) = \begin{Bmatrix} 1 & C_a < 100 \\ 1-b_7C_a & 100 < C_a < 1000 \\ b_8 & C_a > 1000 \end{Bmatrix} \quad (0 \leqslant k_s\,(C_a) \leqslant 1), \tag{8}$$

where $b_7 = (1-b_8)/900$ and b_8 is the minimal value of k_s at values of C_a larger than 1000 cm³/m³.

Interactions

We are uncertain about the extent of the interactions between the variables. We know for example, that k_s of illuminated leaves is reduced by high values of temperature, leaf–air vapour pressure difference, CO_2 concentration and water stress, acting independently. However, we do not know the extent to which k_s is reduced by these variables acting in concert.

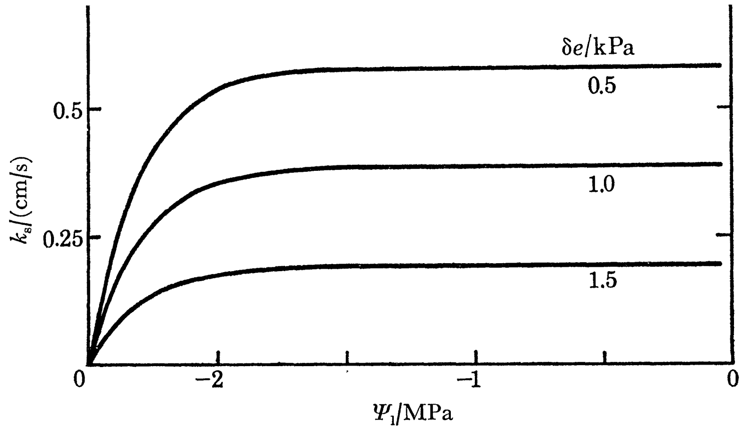


FIGURE 14. The relation between stomatal conductance (k_s) and leaf water potential (Ψ_l) at three levels of vapour pressure difference (δe) as given by equations (7) and (9). Other conditions assumed: T_a = 10 °C; Q_p = 1800 μE m^{-2} s^{-1}; C_a = 300 cm³/m³.

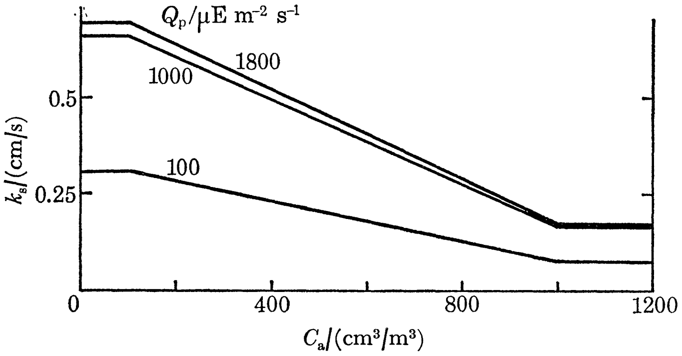


FIGURE 15. The relation between stomatal conductance (k_s) and ambient CO_2 concentration (C_a) at three levels of photon flux density (Q_p) as given by equations (8) and (9). Other conditions assumed: δe = 0.5 kPa; Ψ_l = −0.5 MPa; T_a = 10 °C.

The simplest hypothesis, which we have adopted, is that the k_s obtained is the result of complete expression of the influence of all the variables without any synergistic interactions, namely:

$$k_s\,(Q_p,\,T,\,\delta e,\,\Psi_l,\,C_a) = k_s\,(Q_p)\,k_s\,(T)\,k_s\,(\delta e)\,k_s\,(\Psi_l)\,k_s\,(C_a). \tag{9}$$

That is to say, if k_s is reduced to 80% of maximum by the prevailing photon flux and to 80% of maximum by the prevailing temperature, the resulting k_s will be 64% of maximum k_s. Further experiments are needed to show whether this hypothesis is adequate.

Determination of parameters

The parameters in the model are b_1, b_2, T_l, T_0, T_h, b_5, b_6, Ψ_m and b_7. They are estimated by the simultaneous solution of equations (4) and (8) using nonlinear least squares regression analysis (Draper & Smith 1966). The technique used is identical with that used by Reed *et al.* (1976) to determine the parameters in a CO_2 uptake model and has the same limitations discussed by them. In particular, some bias in the estimated parameters results if the variables do not adequately fill the variable space as shown in figure 16. Such coverage is difficult to obtain in the field where photon flux, temperature and vapour pressure difference, for example, tend to be correlated. Consequently, sampling in the field and the selection of data for the analysis must be arranged deliberately to provide data which are uniformly distributed as far as is possible. If this is not possible, the shoot environment in the field must be artificially controlled to break the correlation between the weather variables and to provide combinations of infrequently occurring conditions in the 'corners' of the variable space.

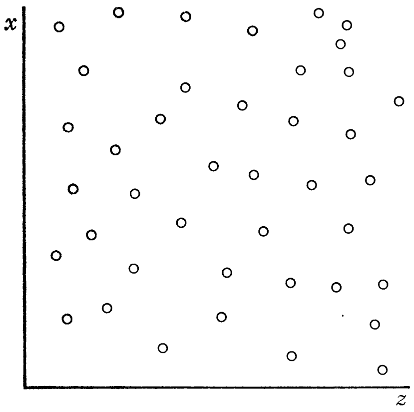


FIGURE 16. A diagram to show the ideal distribution of measurements of stomatal conductance in relation to two driving variables x and z. The measurements are more of less uniformly distributed throughout the variable space.

Application

The model has been used to interpret two sets of measurements of k_s which were collected independently on different species by different techniques.

Data set I: 80 measurements of k_s on current year shoots of Sitka spruce (*Picea sitchensis*) in the upper part of the canopy made with a null-balance, diffusion porometer (Beardsell, Davidson & Jarvis 1972) by W. R. Watts at Fetteresso Forest, U.K., between 25 April–17 May 1973. Concurrent measurements included the driving variables Q, T, δe and Ψ_l but not C_a which was taken as constant.

Data set II: 113 measurements of k_s on current year shoots of Douglas fir (*Pseudotsuga menziesii*) in the middle part of the canopy made with an assimilation chamber (Leverenz 1974) by J. Leverenz at the Cedar River Forest, Washington, U.S.A., between 8 August to 11 September, 1973. Concurrent measurements included all the driving variables.

The parameters determined are listed in table 1. There was insufficient range of variation in some of the variables to allow determination of the bracketed parameters which were fixed at the indicated values. The model accounted for 51 % of the variation in data set I and 73 % of the variation in data set II.

There are substantial differences in the derived parameters between data sets I and II. The Sitka spruce (data set I) had a higher maximum k_s (b_1), a lower temperature optimum for k_s (T_0), a steeper rise in k_s with increasing photon flux density (b_2), a steeper decline in k_s with increasing vapour pressure difference (b_5) and a more abrupt decline with decreasing leaf water potential (b_6). These differences in the parameters may result from differences between the species but more probably describe differences in the physiological condition of the trees in the spring and autumn at the two sites.

TABLE 1. VALUES OF THE PARAMETERS DERIVED FROM APPLICATION OF THE MODEL

quantity	symbol	data set		unit
		I	II	
maximum k_s	b_1	0.43	0.30	cm s^{-1}
$\mathrm{d}k_s/\mathrm{d}Q_p$; $Q_p = 0$	b_2	0.0296	0.0135	(cm s^{-1})/(μE m^{-2} s^{-1})
k_s; $Q_p = 0$	b_{10}	0	0.01	cm s^{-1}
low temperature for $k_s = 0$	T_l	(−5.0)	(−5.0)	°C
temperature for max. k_s	T_0	9.0	20.0	°C
high temperature for $k_s = 0$	T_h	(35.0)	(45.0)	°C
$\mathrm{d}k_s/\mathrm{d}(\delta e)$	b_5	−0.26	−0.12	kPa^{-1}
$\mathrm{d}k_s/\mathrm{d}\Psi_l$; $k_s = 0$	b_6	−40	−0.93	MPa^{-1}
Ψ_l; $k_s = 0$	Ψ_m	(−2.4)	(−2.4)	MPa
$\mathrm{d}k_s/\mathrm{d}C_a$	b_7	(0)	(0)	(cm^3/m^3)$^{-1}$
	R^2	0.51	0.73	

TABLE 2. RANGE OF ENVIRONMENTAL VARIABLES IN DATA SETS I AND II

	data set	
	I	II
photon flux density/(μE m^{-2} s^{-1})	15–1958	34–1831
temperature/°C	7.0–10.0	12.6–42.8
vapour pressure deficit/kPa	0.28–0.52	0.09–5.26
leaf water potential/MPa	0.71–1.62	0.72–2.20
ambient CO_2 concentration/(cm^3/m^3)	300	310–343

The rather low proportion of the variation accounted for in data set I might be attributed to inadequacies in the model. However, plots of the residuals (predicted k_s − measured k_s) with respect to the driving variables show that the positive and negative erros are, in general, equally distributed each side of zero (see figures 16 and 17, for example). Consequently, the low values of R^2 are more likely to reflect inadequacies in the distribution of the data than inadequacies in the model. Both sets of field results have pronounced limitations. The range of the variables T, δe and Ψ_l in data set I is very small (table 2). Whilst a broad range of a variable does not necessarily imply an ideal distribution for parameter estimation, a narrow range is unlikely to be satisfactory. The ranges of the variables are much wider in data set II but certain of the variables are very strongly correlated one with another: extreme values of Q, T, δe and Ψ_l all occur together. Consequently, k_s is small at even moderate levels of any one of the driving variables. For example, k_s does not exceed 0.1 cm s^{-1}, at photon flux densities above 400 μE m^{-2} s^{-1}, or at temperatures higher than 19 °C. Application of the CO_2 uptake model of Reed *et al.* (1975) to similar poorly distributed sets of data also results in low values of R^2, whereas values of R^2 in excess of 0.95 have been obtained with data more uniformly distributed through the variable space. A preliminary test of this model using steady state measurements of stomatal conductance made in the laboratory on forest shoots or potted plants (Ludlow & Jarvis 1971, Neilson *et al.* 1972, Cornic & Jarvis 1972, Neilson & Jarvis 1975), has shown that the model can account for 95% of the variation in the data. Consequently we are now developing the

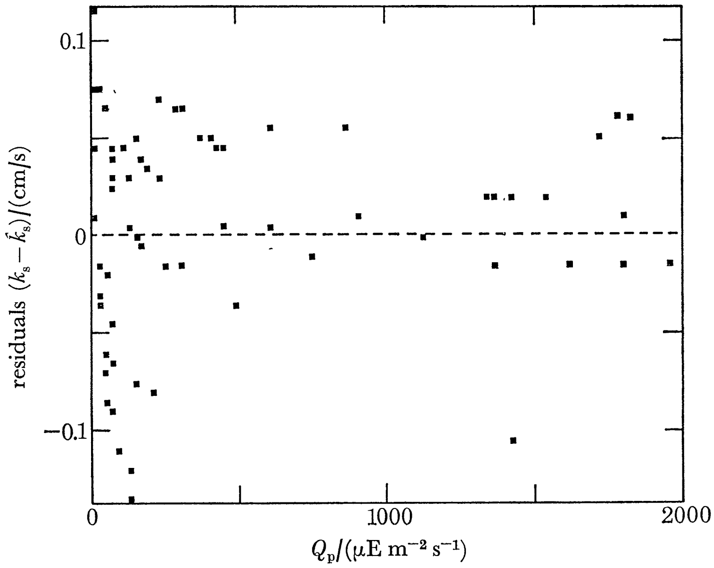


FIGURE 17. The distribution of the differences between stomatal conductance predicted from equations (4) to (9) ($\hat{k}_s$) and measured values of stomatal conductance (k_s) in relation to photon flux density (Q_p). Measurements made at Fetteresso Forest, Spring 1973, on current year's shoots of Sitka spruce in the upper part of the canopy. (Data from Watts, Neilson & Jarvis 1976.)

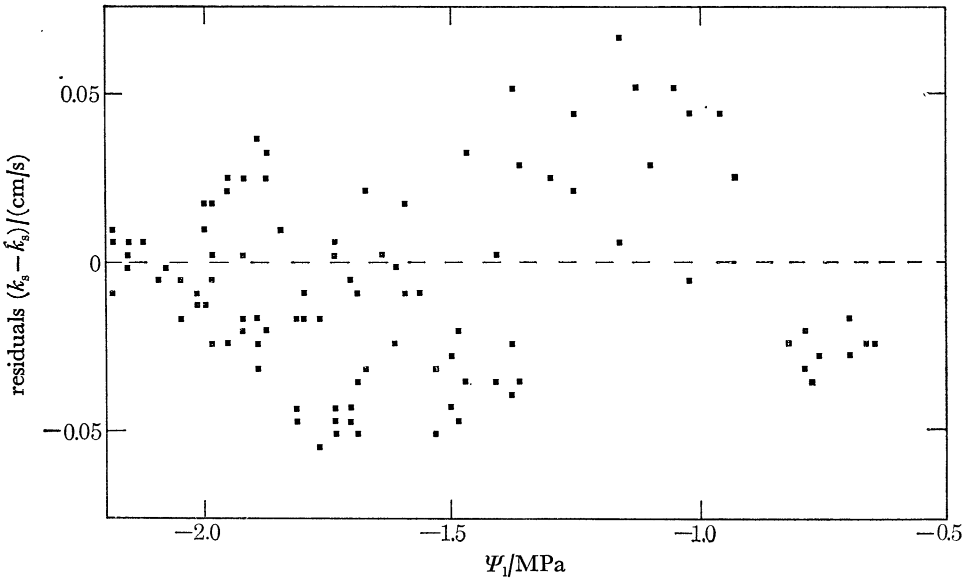


FIGURE 18. The distribution of the differences between stomatal conductance predicted from equations (4) to (9) ($\hat{k}_s$) and measured values of stomatal conductance (k_s) in relation to leaf water potential (Ψ_l). Measurements made at Cedar River Forest, Autumn 1973, on current year's shoots of Douglas fir in the middle of the canopy. (Data from Leverenz 1974.)

use of this kind of analysis to derive seasonal variation in stomatal properties from measurements of k_s made in the canopy at Fetteresso over the last three years.

Interpretation of the response of stomata to environmental variables in this way is practically useful, in that the parameters can be used to make predictions, but it is not wholly satisfactory. The parameters have limited physiological meaning because the model is descriptive rather than mechanistic. Nonetheless, the parameters provide a better description of the properties of the stomata than can be obtained from multiple regression coefficients. Furthermore, as the model evolves to become more mechanistic, it should become possible to interpret the parameters at the process level. We consider that approach outlined here to be a useful interim way of using measurements made in the field to describe the changing properties of the stomata.

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