

RELATION TO LEAF METABOLISM
AND ENVIRONMENT

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INTEGRATION OF ACTIVITY
IN THE HIGHER PLANT

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STOMATAL FUNCTION IN THE
REGULATION OF GAS EXCHANGE

It is proper to enquire, first, what stomata do; secondly, how they do it; and only then, if the question is allowed at all, why they do it. There are excellent reviews (e.g. Raschke, 1975a) which deal with stomatal physiology in this way. Here we propose to adopt a different sequence: first, to make an assumption about the role of stomata, to explore the implications of that assumption in terms of stomatal behaviour, and then to enquire whether and how that behaviour is realised in practice.

We suppose that the function of stomatal activity is to minimise loss of water from the plant. Clearly, minimisation with respect to time is meaningless: that would demand that stomata remain continuously closed. The appropriate scale is not time, but plant growth, or development. Nevertheless time does enter the problem. It is impracticable, however desirable it might be in principle, to discuss how stomatal behaviour might minimise loss of water over the entire life cycle of a plant. Instead we equate growth and development with assimilation, and assume that stomata function so that the total loss of water during a day is a minimum for the total amount of carbon taken up. That is the basic hypothesis. Stomatal behaviour which conforms to it will be called 'optimal'.

Imagine that we could perturb stomatal aperture at will, without changing the environment or causing a change in plant physiological characteristics. Let δE and δA be the corresponding fluctuations in rate of transpiration and rate of assimilation per unit area of leaf. Then the unperturbed diurnal course of stomatal behaviour is optimal if

$$\int \delta E dt \geq 0 \quad (1)$$

for all sequences of perturbations such that

$$\int \delta A dt = 0, \quad (2)$$

the integrals encompassing the entire day. The criterion stated in this way can hardly form the basis of a viable experiment and we shall defer, until later, discussing how the hypothesis might be tested. Our main approach will be to establish relationships for the dependence of E and A on stomatal aperture, to show what the optimal time courses of stomatal aperture, rate of transpiration, and rate of assimilation must then be for certain environmental and plant physiological characteristics, and to discuss these computations in the light of observations with real plants. Much of the relevant theory has been developed by Cowan & Troughton (1971), Farquhar (1973) and Cowan (1977), but was applied using a very simplified model, only, of CO_2 exchange in leaves.

TRANSPIRATION

Leaf resistance to transpiration, a property of the epidermis depending mainly on the number and dimensions of the stomatal pores, is defined as r_1 in

$$E = \frac{w_1 - w_a}{r_1 + r_b}, \quad (3)$$

where E is rate of transpiration per unit area of leaf, w_1 and w_a are the humidities of the air in the intercellular spaces and ambient air, respectively, and r_b is the resistance of the boundary layer to transfer of water vapour. With w expressed in moles water vapour per mole air (numerically approximate to vapour pressure expressed in bars (10^5 Nm^{-2})) and E in $\text{mol m}^{-2} \text{ s}^{-1}$, resistance has units of $\text{m}^2 \text{ s mol}^{-1}$; its reciprocal, conductance, has the same units as E . The advantage of using these units has been discussed elsewhere (Cowan, 1977). A resistance of $1 \text{ m}^2 \text{ s mol}^{-1}$ is roughly equivalent to a resistance, in the units commonly used, of 0.4 s cm^{-1} .

In using equation (3) to determine r_1 it is commonly assumed that $w_1 = w'(T_1)$, the humidity of air saturated at leaf temperature, T_1 . In computing the influence of r_1 on rate of transpiration another inter-relationship between E and T_1 has to be taken into account: that which relates to the energy balance of the leaf. The two relationships may be expressed as

$$E = \frac{w'(T_1) - w_a}{r_1 + r_b} = \frac{1}{L} \left\{ \phi_0 - 2\sigma(T_1^4 - T_a^4) - \frac{C_p(T_1 - T_a)}{1.12 r_b} \right\}, \quad (4)$$

where L is the molar heat of vaporisation of water; ϕ_0 is the net radiation that would be received per unit leaf area were leaf temperature that of the ambient air, T_a ; σ is the Stefan-Boltzmann constant; and C_p is the molar

heat capacity of air. The numerical factor 1.12 derives from the theory of heat and mass transfer in laminar boundary layers. Frequent use is made of approximate solutions of equations (4) for E and T_1 , the functions $w'(T)$ and T^4 having been taken as linear over the range T_1 to T_a . As our overall analysis demands the use of a digital computer, we have preferred to obtain accurate solutions by progressively adjusting the magnitude of T_1 until the two expressions for E are in close numerical agreement.

ASSIMILATION

Rate of assimilation may be written

$$A = \frac{c_a - c_1}{1.35r_b + 1.6r_1} = A(c_1, T_1, I). \quad (5)$$

The first of the expressions for A need not detain us long; c_a and c_1 are the concentrations of CO_2 in the ambient atmosphere and the intercellular airspaces in the leaf, respectively, and the numerical factors represent the influence of the molecular diffusion coefficient of CO_2 in air, relative to that for water vapour, on transfer through the boundary layer and through the stomata. Consistent with equation (4), c is to be expressed in $\text{mol CO}_2 \text{ mol}^{-1}$ air (for all practical purposes identical with volume fraction) and A in $\text{mol m}^{-2} \text{ s}^{-1}$. The second expression relates to the fact that uptake of CO_2 by leaf mesophyll is predominantly a function of c_1 , T_1 , and the irradiance, I . Of course the function may be affected by other factors such as water potential, and it may be affected by the preceding history of assimilation in the leaf, as this will have affected the pool sizes of metabolites. We shall ignore these possibilities for the time being.

A comprehensive determination of $A(c_1, T_1, I)$ for any one species has yet to be made. Here we rely on the model of photosynthesis in C_3 species of Hall (1971), as extended by Hall & Björkman (1975), to generate hypothetical response characteristics. Fig. 1 shows rate of assimilation as a function of intercellular concentration of CO_2 , and leaf irradiance, at 27°C leaf temperature. The parameters of the model are those adopted by Hall based on data relating mainly to *Atriplex patula*. In taking account of the influence of leaf temperature, Hall & Björkman assume that certain parameters of the model may be represented by an Arrhenius-type function with an activation energy of 16 kcal mol^{-1} below 27°C and 10 kcal mol^{-1} above. We have introduced a slight modification. We take the larger activation energy as appropriate at all temperatures for the photorespiratory parameter, R , and the rate of dark respiration, R_d , and the smaller energy as appropriate at all temperatures for the other temperature-sensitive

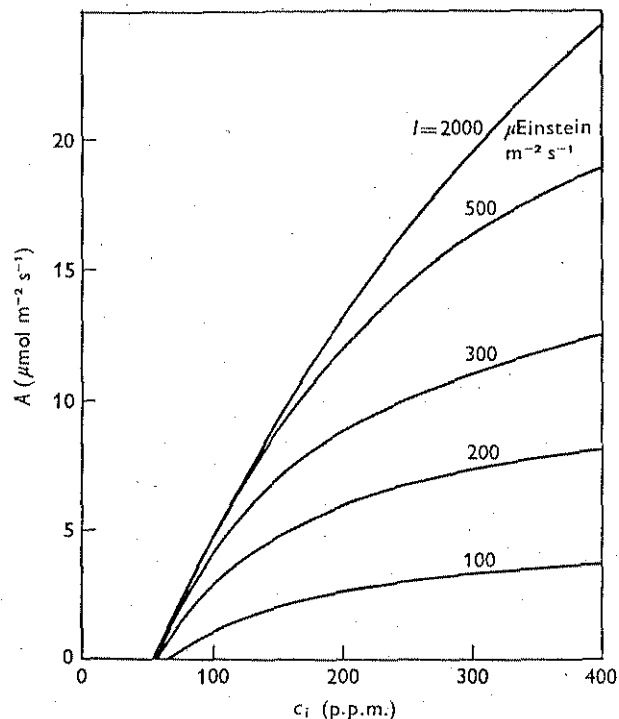


Fig. 1. Rate of assimilation, A , as a function of intercellular CO_2 concentration, c_i , and irradiance, I , at leaf temperature 27°C . Derived from the model of Hall & Björkman (1975).

parameters, namely r'_{k_1} , P_x and P_m . This arbitrary change has the dual advantages of removing a discontinuity that would unduly affect our analysis, and yielding somewhat more realistic variations with temperature of certain gross properties, such as those shown in Fig. 2. The magnitudes of Γ , CO_2 concentration at compensation, are characteristic of what is observed with C_3 species, and the rate of assimilation with large irradiance and normal ambient concentration of CO_2 , though it varies insufficiently with temperature, has a maximum – in contrast with the unadulterated model – which is within the range of physiological temperatures. We are grateful to Dr A. E. Hall for comments relevant to the continued improvement of models of photosynthesis. We have not attempted to incorporate theoretical modifications here, as we do not believe they would have a qualitative effect on our analysis of optimisation. For certain purposes we require a set of characteristics consistent with a leaf having a smaller capacity for assimilation. We have doubled the magnitude of the 'resistance' r'_{k_1} , and halved the magnitudes of the 'fluxes' P_x , P_m , R and R_d to obtain the curves shown in Fig. 3.

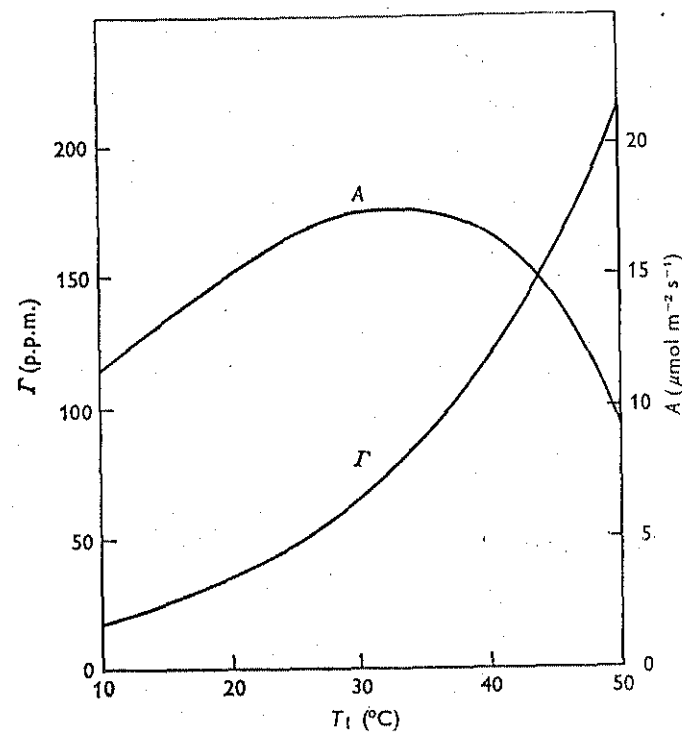


Fig. 2. CO_2 compensation point Γ , and assimilation rate A (at a saturating irradiance, normal ambient concentration of CO_2 and leaf conductance $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$), as functions of leaf temperature, T_l . Derived using the model of Hall & Björkman (1975).

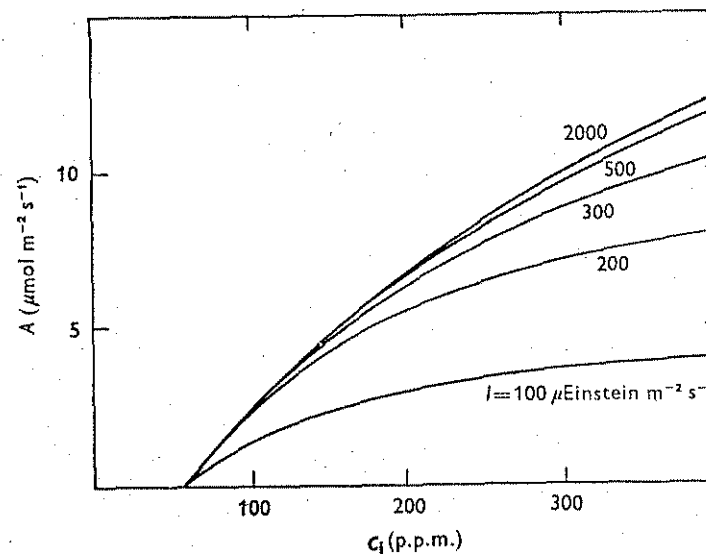


Fig. 3. As Fig. 1 but with certain parameters in the model of Hall & Björkman (1975) changed as described in the text.

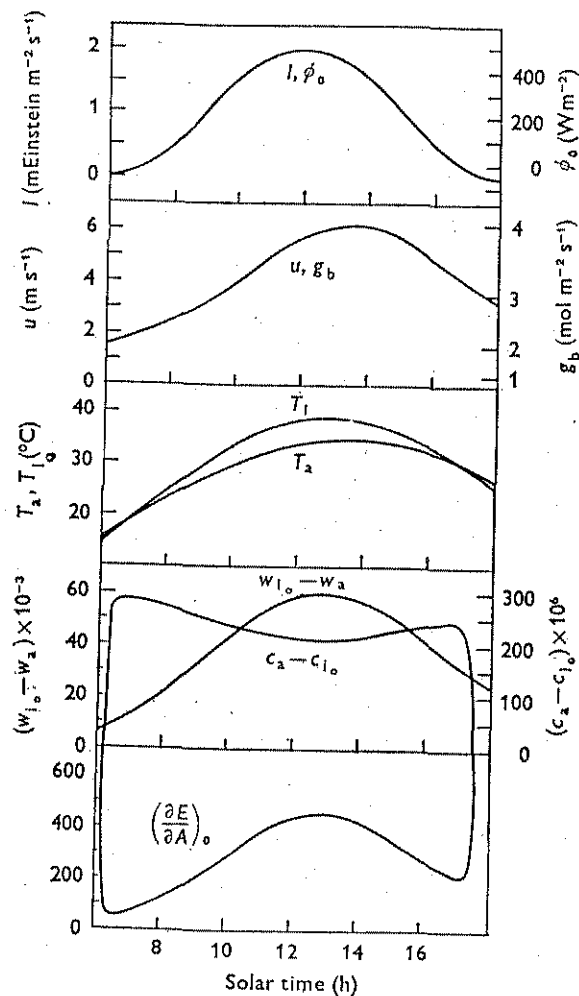


Fig. 4. Assumed diurnal variation in climatic variables together with certain dependent physiological variables. I , ϕ_o , u , g_b , and T_a are, respectively, irradiance, net radiation, windspeed, leaf boundary layer conductance and air temperature. $w_{l_0} - w_a$ and $c_a - c_{l_0}$ are, respectively, the differences in humidity and CO_2 concentration across the leaf epidermis and boundary layer, computed assuming that leaf conductance is zero. $(\partial E/\partial A)_o$ is the corresponding limiting magnitude of the transpiration ratio.

CLIMATE

Fig. 4 shows the idealised course of leaf microclimate which has been used as the basis for subsequent computations. Except with respect to the smoothness of the variables, it might represent conditions experienced by a more or less horizontal leaf in an arid semi-tropical region. The irradiance,

I , is appropriate for a cloudless sky. The net radiation, ϕ_o , is based on an absorption coefficient for solar radiation of about 0.6 and a constant net loss of thermal radiation of 50 W m^{-2} . The relationship between the conductance of the boundary layer, $g_b = 1/r_b$, and windspeed, u , stems from laminar flow theory (Cowan, 1972a) and relates to a leaf 40 mm broad. It is windier, and the air temperature, T_a , is greater, in the afternoon than the morning. The other variables illustrated in Fig. 4 are derived in the way now to be discussed.

Given the basic microclimatic information in Fig. 4, together with the characteristics of assimilation which are illustrated in Fig. 1, then equations (4) and (5) may be used to determine how E and A depend, at any given time of the day, on leaf conductance g_1 . It is useful first to consider the solution for very small magnitudes of g_1 . It is found that

$$E \approx (w_{l_0} - w_a) \cdot g_1, \quad (6)$$

where $w_{l_0} = w'(T_{l_0})$, T_{l_0} being the leaf temperature found by setting the second expression for E in equation (4) equal to zero. Further

$$A \approx (c_a - c_{l_0}) \cdot g_1 / 1.6, \quad (7)$$

where c_{l_0} is the internal CO_2 concentration such that $A(c_{l_0}, T_{l_0}, I) = 0$. When the irradiance is large $c_{l_0} = \Gamma(T_{l_0})$, the compensation concentration. It follows from equations (6) and (7) that

$$\lim_{g_1 \rightarrow 0} \left(\frac{E}{A} \right) = \left(\frac{\partial E}{\partial A} \right)_o = 1.6 \frac{(w_{l_0} - w_a)}{(c_a - c_{l_0})}. \quad (8)$$

It is to be emphasised that the partial differential represents change in rate of transpiration with change in rate of assimilation at a given time, and it is leaf conductance, and not climate, which implicitly (but infinitesimally) changes. The variables T_{l_0} , $w_{l_0} - w_a$, $c_a - c_{l_0}$, and $(\partial E/\partial A)_o$ are shown in Fig. 4 (w_a having been taken as 10^{-3} and c_a as 320×10^{-6}). These curves indicate the nature of our problem. If the plant is to assimilate only a small amount of CO_2 , it is evident that, to expend the least possible amount of water, it should do so when $(\partial E/\partial A)_o$ is least. But if it is to assimilate a substantial amount, then it is not evident how it should distribute its activity during the course of the day, for w_1 , c_1 and therefore E/A will be modified in a complex way relating to the actual rate of gas exchange.

OPTIMISATION AS A PROBLEM IN TOPOLOGY

For any given combination of environmental properties, that is to say at any particular instant of time, leaf resistance may be regarded as a

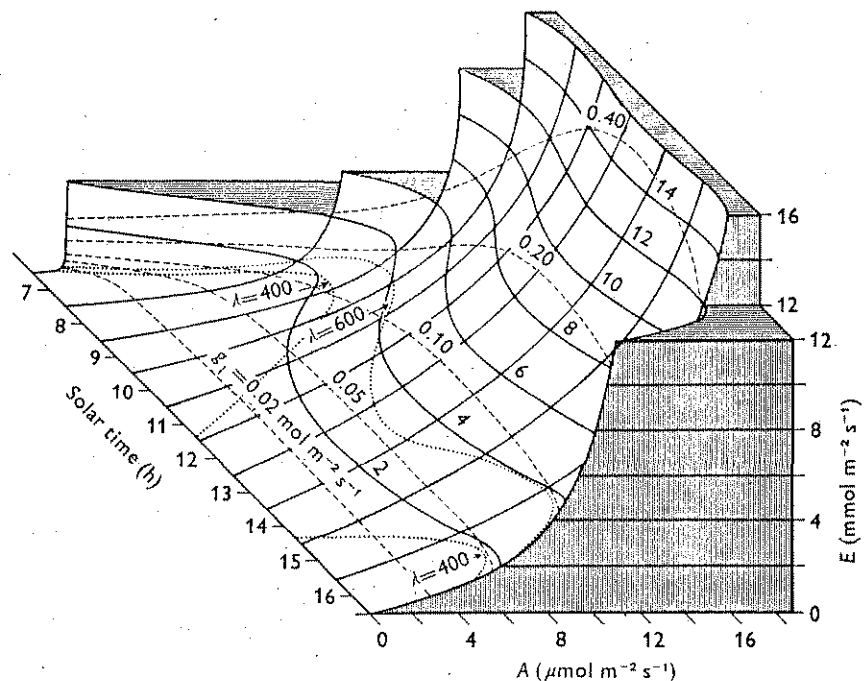


Fig. 5. Rate of evaporation, E , as a function of rate of assimilation, A , and time computed using the metabolic characteristics illustrated in Figs. 1 and 2 and the climatic characteristics illustrated in Fig. 4. The magnitudes of E are indicated on the contours of the surface. The broken lines represent the relationship between E and A for various constant magnitudes of leaf conductance ($\text{mol m}^{-2} \text{s}^{-1}$). The dotted lines represent optimal relationships between E and A .

logical parameter linking equations (4) and (5). If solutions of these equations are found for various magnitudes of r_1 then E can be plotted as a function of A . When the environmental properties are allowed to vary as they do during the course of a day, then E can be plotted as a function of both A and time. This is what has been done in Fig. 5. The contours of the surface represent constant levels of transpiration rate. The broken curves which traverse the surface represent the relationships between E and A for various constant magnitudes of leaf conductance. It is a surface which everywhere increases in slope, $\partial E/\partial A$, as A increases; that is to say it is curved in the sense $\partial^2 E/\partial A^2 > 0$. The minimum slope at any given time is that at the $E = A = 0$ axis and has been defined as $(\partial E/\partial A)_0$ in equation (8). The problem now is to find how the time courses of E and A corresponding to optimal stomatal behaviour traverse the surface. Two optimal trajectories are shown in Fig. 5. They are two of an infinite number, each

of which is defined by the magnitude of a parameter λ according to the relations

$$\frac{\partial E}{\partial A} = \lambda \quad \text{when} \quad \left(\frac{\partial E}{\partial A}\right)_0 \leq \lambda, \quad (9)$$

$$E = A = 0 \quad \text{when} \quad \left(\frac{\partial E}{\partial A}\right)_0 \geq \lambda. \quad (10)$$

Thus an optimal trajectory is a line which joins points of uniform slope λ when it is possible to do so; at times when the minimum slope of the surface exceeds λ then the trajectory is forced to follow the $E = A = 0$ axis, implying that leaf conductance is zero.*

The proof is readily found on the basis of equations (1) and (2). Equation (1) may be rewritten, provided δE is taken to be small

$$\int \delta E dt = \int \left\{ \frac{\partial E}{\partial A} \delta A + \frac{1}{2} \frac{\partial^2 E}{\partial A^2} (\delta A)^2 \right\} dt \geq 0. \quad (11)$$

First consider the case (illustrated in Fig. 5 for $\lambda = 600$) when λ is such that E and A remain finite throughout the day. As $\partial E/\partial A$ is constant the integral of the first term in equation (11) is zero. As $\partial^2 E/\partial A^2$ is positive the integral of the second is of necessity greater or equal to zero. Thus the inequality is satisfied. If $\partial E/\partial A$ were not constant it would be possible to choose a hypothetical sequence of small perturbations δA , conforming to equation (2), such that the first component of the integral in equation (11) would be negative and the second negligibly small. The extension of the proof to encompass cases such as that illustrated by $\lambda = 400$ in Fig. 5 is trivial. When $(\partial E/\partial A)_0 > \lambda$, then $E = A = 0$ simply because g_1 cannot become negative. Any hypothetical perturbation δA must be positive; therefore the first component of the integral in equation (11), though now finite, must also be positive – always provided equation (2) is satisfied.

Of course, we recognise that g_1 cannot in fact become quite zero; even if the stomata are fully closed some gas exchange will continue to take place across the cuticle. This is a minor complication in theoretical terms, fully accounted for if equation (10) is replaced by

$$E = E_0, A = A_0 \quad \text{when} \quad \left(\frac{\partial E}{\partial A}\right)_0 \geq \lambda,$$

* The problem is a degenerate case of what is known, in the calculus of variations, as the 'isoperimetric problem'. The classical treatment is given by Courant & Hilbert (1953) and involves the use of Lagrange multipliers. The parameter λ , used in our treatment, is equivalent to the first Lagrange multiplier, which is conventionally denoted by that symbol. In another treatment (Cowan, 1977) a different symbol was used.

with the subscript 0 indicating quantities corresponding to closed stomata, rather than zero conductance. However, the presence of a finite cuticular conductance is (assuming that it does not discriminate in favour of CO_2 transfer) a physiological imperfection in the context of the theory of optimisation, just as an inability to completely close stomata would be. For this reason we have not attempted to illustrate the effect in Fig. 5. But what of those periods, not incorporated in Fig. 5, during the night, the very early morning, and the very late evening when light intensity is zero, or very small, and there is a net efflux of CO_2 from the leaf? Mitochondrial respiration is not greatly inhibited by CO_2 concentrations of more than 1000 p.p.m., and it may be assumed that cuticular conductance alone is sufficient to prevent internal concentration of CO_2 becoming as great as this. Therefore any influence of leaf conductance is indirect; if the stomata open and the rate of transpiration is increased, then leaf temperature, and therefore rate of respiration, is reduced. It follows that, although A is negative, $\partial E/\partial A$ is positive. We calculate that $\partial E/\partial A$ is likely to be very large under all natural circumstances. That is to say transpirational cooling would be an inefficient means of reducing dark respiration. When the leaf receives some – but very little – light, we suppose that there may sometimes be a tendency for the efflux actually to increase as leaf conductance increases, because a smaller proportion of the CO_2 respired is photosynthesised if c_i is reduced. Therefore conservation of water and conservation of carbon both require that the stomata be closed.

The analysis of optimisation may be generalised to take account of the fact that the different leaves of a plant experience different microclimates and may have different metabolic characteristics. For the whole plant, equations (1) and (2) become

$$\int \sum_j \delta E_j a_j dt \geq 0 \quad (12)$$

for

$$\int \sum_j \delta A_j a_j dt = 0, \quad (13)$$

where δE_j , δA_j are perturbations in a particular leaf, area a_j . For each leaf we may express E_j as a quadratic function of A_j as in equation (11). It follows that the inequality above obtains, for all temporal and spatial variations in A_j which satisfy equation (13), only if each leaf regulates its activity according to equations (9) and (10), the magnitude of λ being the same for all leaves. However, we shall concentrate attention on temporal rather than spatial organisation.

Fig. 6 shows a set of optimal trajectories, in (a) as they appear when projected on to the E, t plane in Fig. 5 and in (b) as they appear when

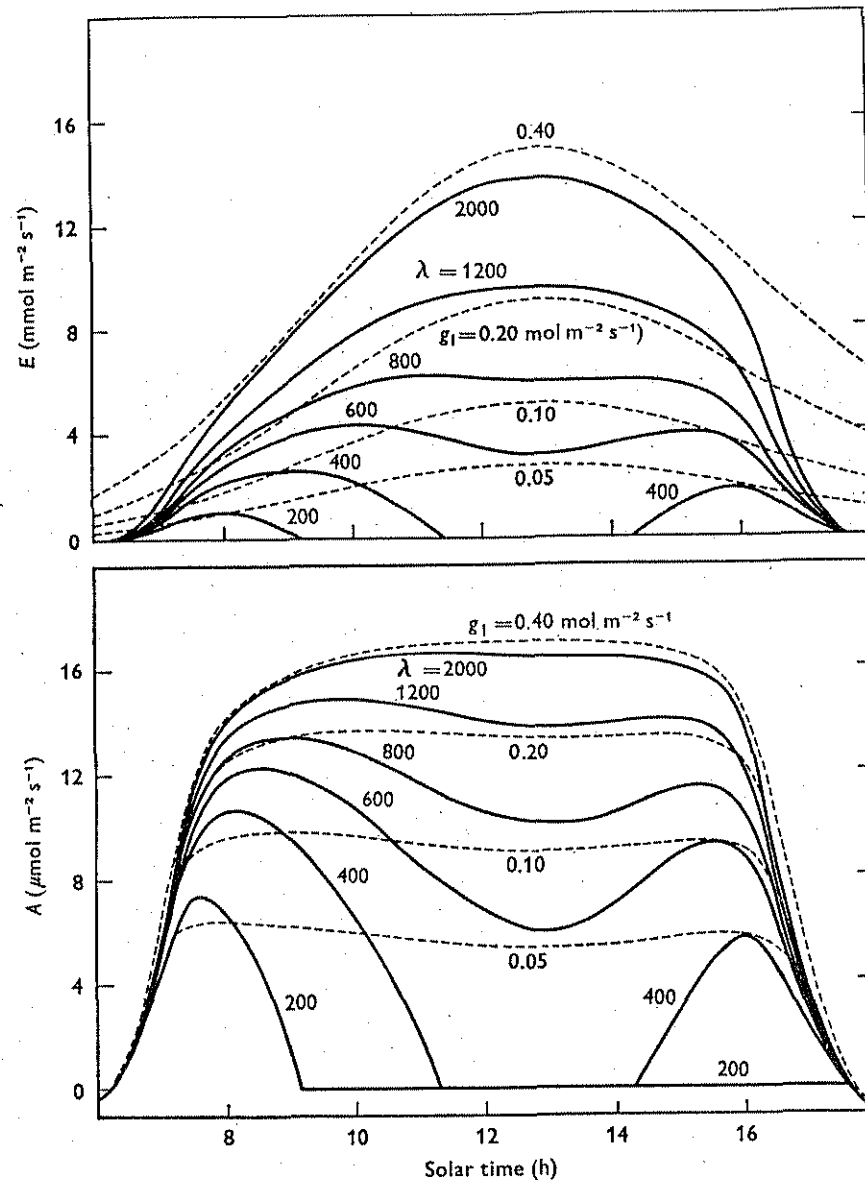


Fig. 6. Optimal time courses of rate of assimilation, A , and rate of evaporation, E for various magnitudes of λ (solid lines). Also shown are A and E for various magnitudes of leaf conductance, g_1 .

projected on to the A, t plane. Each trajectory corresponds to a particular magnitude of λ . As in Fig. 5, the broken curves represent E and A at various constant magnitudes of leaf conductance, g_1 . The larger the magnitude of λ the greater will be the mean rates of transpiration, \bar{E} , and

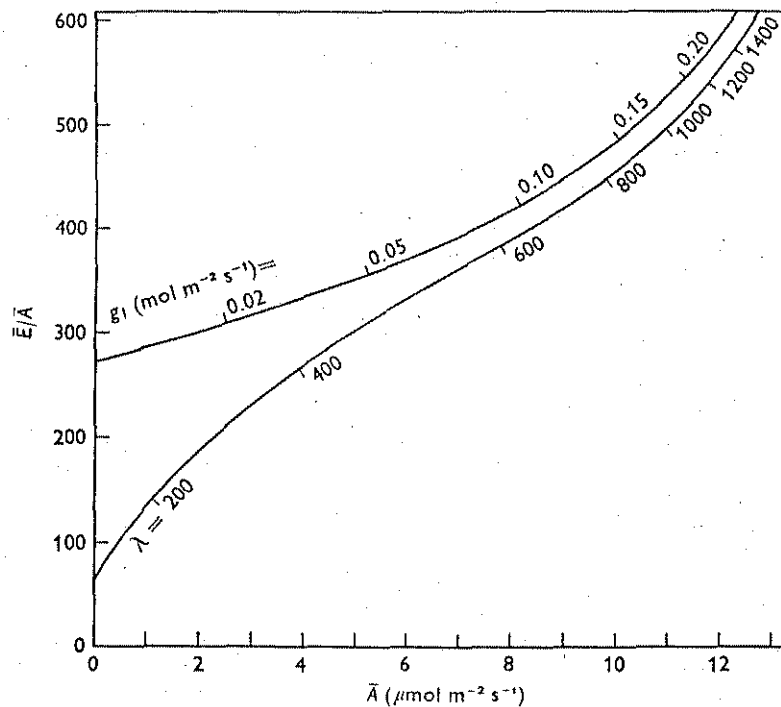


Fig. 7. Ratio of mean diurnal rate of evaporation, \bar{E} , to mean diurnal rate of assimilation, \bar{A} , as a function of \bar{A} . The lower curve is the optimal relationship each point representing a particular magnitude of λ . The upper curve is the relationship corresponding to various constant magnitudes of leaf conductance, g_1 .

assimilation, \bar{A} , and the greater the ratio \bar{E}/\bar{A} . The variation of \bar{E}/\bar{A} with \bar{A} is shown in Fig. 7. It is the 'optimal' relationship, in the sense that each magnitude of \bar{E} is the minimum possible for the corresponding \bar{A} . For comparison, the relationship with leaf conductance, g_1 , rather than λ , being the linking parameter is also shown. Each magnitude of \bar{A} corresponds to a particular constant leaf conductance. The vertical displacement of the two curves is a measure of the benefit obtained in terms of water economy by optimisation of stomatal behaviour. It may appear not to be great, but of course we have no means of translating the difference in terms of selective advantage. And, as we shall discuss later, the fact that the difference is small at large magnitudes of \bar{A} has interesting implications.

THE SIGNIFICANCE OF THE PARAMETER λ

It would be tedious to explore in detail the influence of all relevant factors on the shapes of optimal stomatal trajectories. For the purposes of the ensuing discussion it is necessary only to recognise that the factors are of

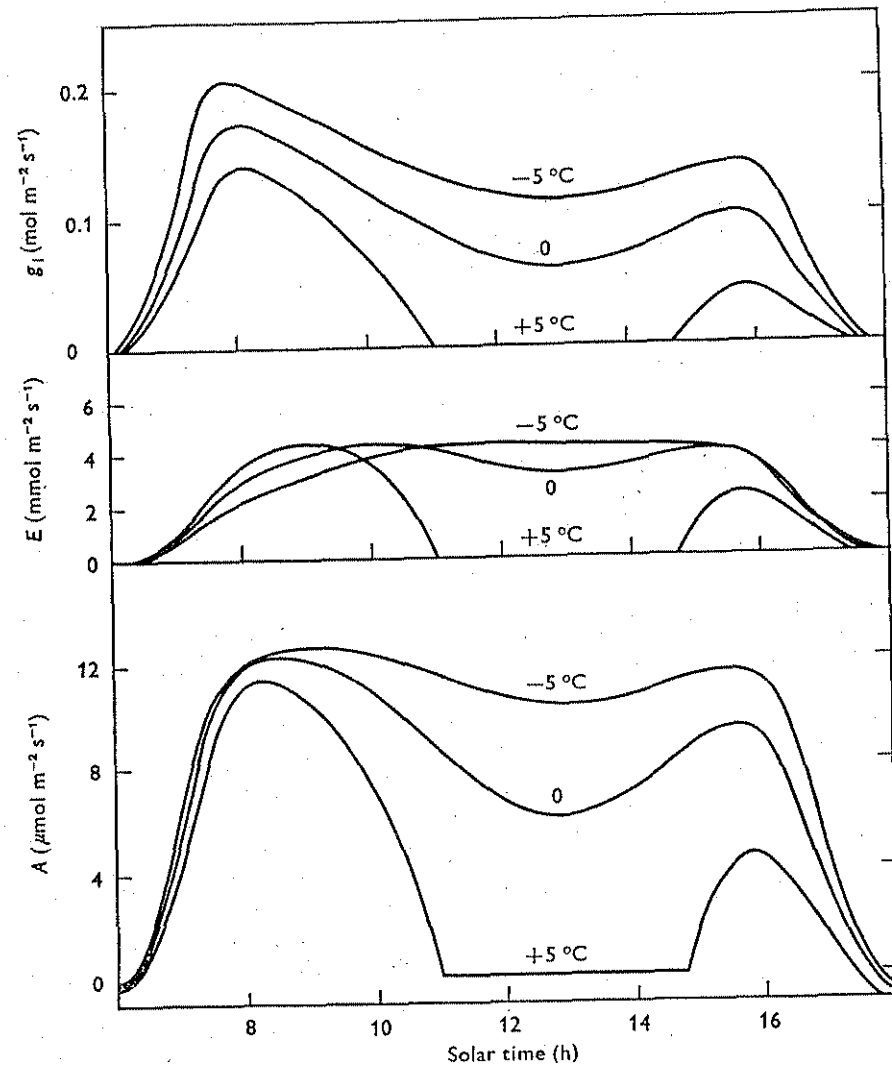


Fig. 8. Optimal time courses of rate of assimilation, A , rate of evaporation, E , and leaf conductance, g_1 , for $\lambda = 600$. The curves marked \circ correspond to the climate in Fig. 4. The other curves are associated with ambient air temperature 5°C hotter in the one case, and 5°C cooler in the other.

three kinds. We have seen, first, that the trajectory is influenced by the magnitude of the parameter λ . Secondly, we now note that for any given magnitude of λ the trajectory is different for different environments. Fig. 8 shows how the trajectory $\lambda = 600$ is affected if we take ambient air temperature to be 5°C cooler in the one case, and 5°C hotter in the other, than that shown in Fig. 4. And, thirdly, for any given magnitude of λ and any given environment the trajectory is different for plants having different

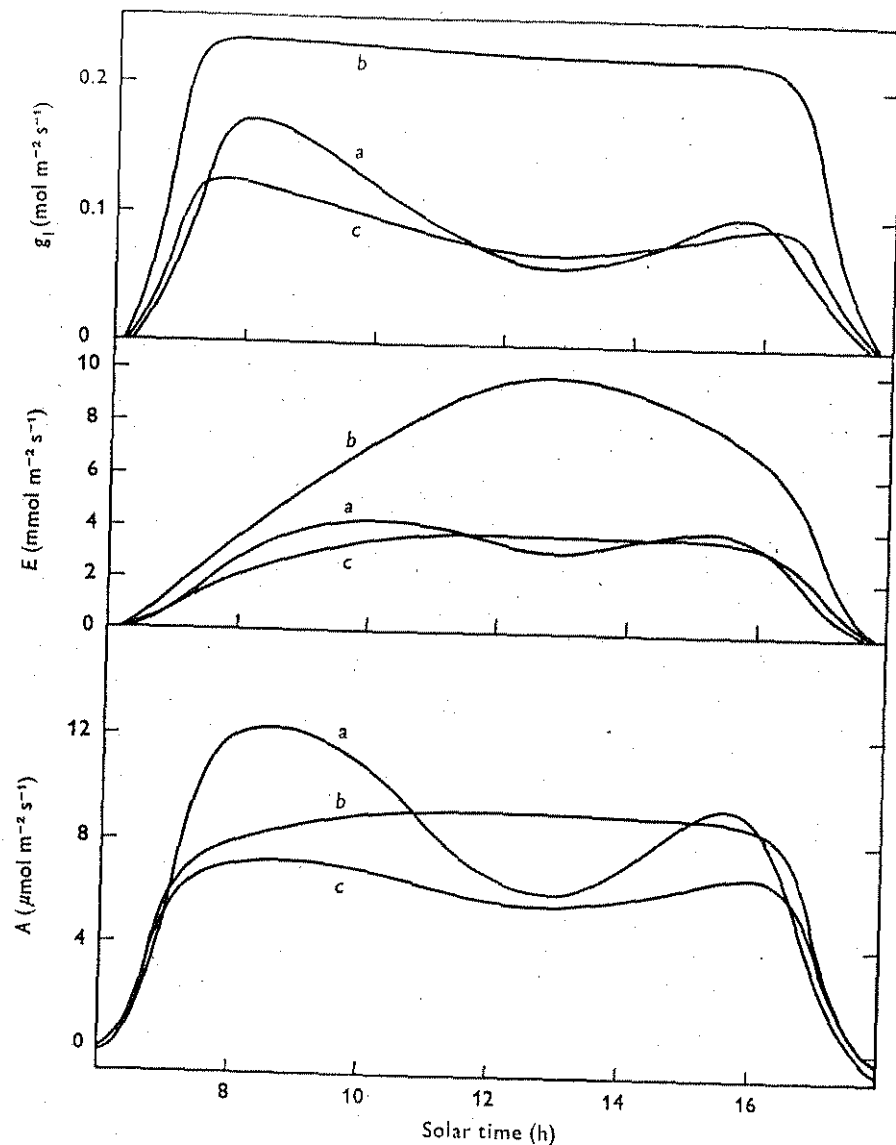


Fig. 9. Optimal time courses of rate of assimilation, A , rate of evaporation, E , and leaf conductance, g_l . The curves marked a correspond to the metabolic characteristics shown in Fig. 1 and $\lambda = 600$. The curves marked b and c are associated with the metabolic characteristics shown in Fig. 3, and $\lambda = 3200$ and 1000 , respectively.

metabolic characteristics. Fig. 9 indicates how optimal behaviour is affected if computations are based on the characteristics shown in Fig. 3 rather than those in Fig. 1.

It is not difficult to appreciate that the optimal diurnal course of stomatal

behaviour is influenced by environment and plant metabolism. But what is the significance of λ ? The degree of freedom that it allows in our computations has not been identified with a climatic or physiological source. Our theory does not provide any indication of what the magnitude of λ should be. It suggests, only, that a given requirement for assimilate is satisfied with the least possible loss of water if the plant adopts a diurnal pattern of activity corresponding to a particular magnitude of λ . The larger the requirement the greater λ should be. Conversely, a given expenditure of water is accompanied by the greatest possible uptake of CO_2 if the plant adopts an activity corresponding to a particular magnitude of λ . The greater the expenditure that can be tolerated the greater λ should be. For a particular diurnal variation of climate there is a unique relationship between \bar{A} , \bar{E} and λ , as illustrated in Fig. 7. But of course climate is unpredictable and if a plant were to 'choose' a particular magnitude of λ and regulate its stomatal behaviour to conform with equations (9) and (10) it could have no 'knowledge' *a priori* of the magnitudes of \bar{A} and \bar{E} that would result from that choice. If, therefore, λ has biological significance, it is that of a plant physiological parameter fashioned by evolution in the context of an environment having certain statistical properties.

If the principles we have derived are applicable to transpiration and assimilation during a single day, then they might seem also to be applicable over longer periods of time. After all, the range of the integral in equation (11) is arbitrary. Is it possible that λ is constant for a given species, stomatal behaviour changing from day to day as climatic conditions change, and changing, also, as metabolic characteristics change with leaf age, but always in conformity with the ordained magnitude of λ ? There are several reasons for rejecting this possibility; a brief discussion of them may help to clarify the nature of λ .

Plant metabolism and environment, together, have been regarded as an independent system. Fig. 5 represents the relationship between input, A , and output, E . But in fact the parameters of the metabolic component of the system are themselves changed by the nature of the input. Put simply, the shape of the response surface in Fig. 5 during the afternoon may be affected by the particular amount of carbon taken up during the morning. We have disregarded this possibility. However, there can be no doubt that the amount of carbon taken up during one week will have a significant influence on the size and development of the plant during the next, so that in the longer term, the influence of rate of assimilation on rate of increase in leaf area and development of the plant cannot be ignored. A more complex analysis of optimisation, based on the assumption that rate of increase in leaf area is directly proportional to rate of assimilation, leads

to the conclusion that minimisation of water loss for a given amount of assimilation (and therefore increase in leaf area) in a given period of time requires that λ decrease continuously. But of course the assumption is an oversimplified description of vegetative growth, and the analysis suffices only to indicate that λ is unlikely to remain invariant.

The second reason for supposing that λ is not constant in time relates to the stochastic nature of the climatic component of the 'system'. Sometimes a fixed λ would prove to be unnecessarily conservative for a particular plant in a particular environment, as in a season having more, or more frequent, rain than usual. Sometimes it would be insufficiently conservative and dehydration would cause irreversible physiological damage. The chance that a given magnitude of λ will prove in retrospect to have been optimal for growth and reproduction in an individual plant is remote. Is a given constant magnitude of λ likely to be optimal for the success of a whole population of plants? We can see immediately that it is not. If, because of particular environmental circumstances, those plants which happen to exhaust the supply of water available to them have the capability of closing their stomata and maintaining their integrity to the extent that they may grow and reproduce when water is again available, then both the individuals and the population are so much better fitted to survive. But closure of stomata is represented by $\lambda \rightarrow 0$ in the present context. It is a small step only to appreciate the advantages of an λ which declines continuously as the availability of water diminishes. Unpublished data of H. Rawson are consistent with this general pattern.

In brief, we visualise λ as a parameter which varies over periods which are significant in terms of the relative growth and ontogenetic development of a plant, and is affected also by changes in the water relations of the plant insofar as they are determined by the state of water in the ground. Diurnal changes in the development of a plant, and the amount of ground water available, are usually quite negligible, while the variation of environment encountered by the aerial parts is greater than the variation of the mean daily climate over the whole year. It is for this reason that we argue that the grand strategy associated with water relations and carbon metabolism is likely to degenerate to a tendency for $\partial E/\partial A$ to be constant during a single day.

Superficially, curves of the type shown in Fig. 6 bear a resemblance to observations of gas exchange with plants in the field. Fig. 10, from Lange *et al.* (1975), shows the diurnal course of assimilation rate in wild species in the Negev desert at different times of the year. It is tempting to suppose that the successive changes in the shape of the curve for each individual species are primarily a reflection of changes in λ . But we have no way of knowing whether the shape of each individual curve is consistent with the

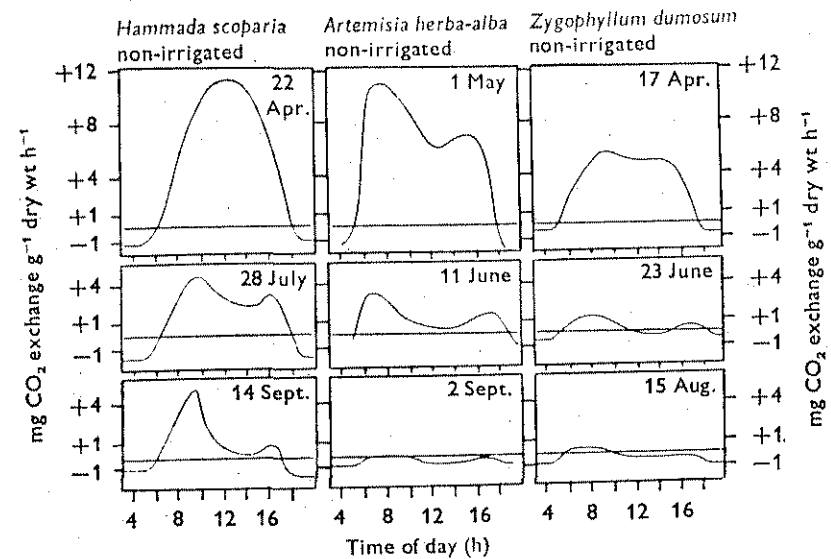


Fig. 10. Diurnal course of net photosynthesis of natural-growing *Hammada scoparia*, *Artemisia herba-alba*, and *Zygophyllum dumosum* in the different seasons in 1971. (From Lange *et al.*, 1975.)

supposition that $\partial E/\partial A$ tends to be constant during the day, because we do not have the necessary basic information about the metabolic characteristics of these species. Indeed none of the many excellent investigations of leaf conductance and gas exchange in the field have been supported by sufficient physiological information to allow a test of our proposition. In Appendix II we show how $\partial E/\partial A$ could be determined, but for the present we must make do with circumstantial evidence only.

THE PHYSIOLOGICAL MECHANISM OF OPTIMISATION

The theory outlined provides a means by which we may estimate the time course of optimal stomatal behaviour in a particular set of circumstances. It does not purport to indicate how the plant may set about the task. But our theory would become more plausible if we could at least show that the nature of observed stomatal response to external environmental variables and internal physiological variables is consistent with the possibility of optimisation. We base our discussion on Fig. 11, which shows leaf conductance, together with certain external and internal variables, corresponding to the curves for $\lambda = 600$ in Fig. 6. Appendix II contains a formal, more general treatment of the matters discussed in this section.

Until quite recently the dominant influences on stomatal aperture were

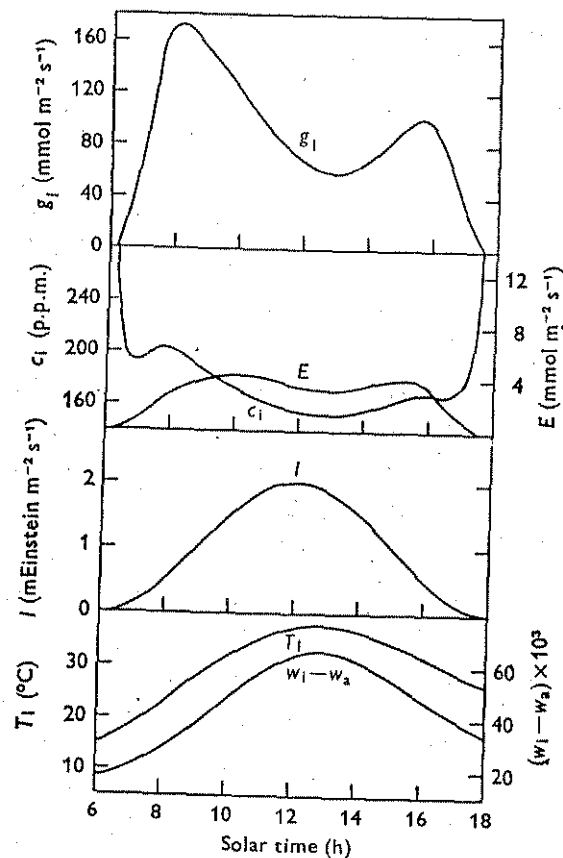


Fig. 11. Diurnal course of optimal leaf conductance, g_l , rate of evaporation, E , intercellular CO_2 concentration, c_l , irradiance, I , leaf temperature, T_l , and difference between internal and ambient humidity, $w_l - w_a$, corresponding to the optimal curve $\lambda = 600$ in Fig. 5.

thought to be leaf intercellular CO_2 concentration, and internal water relations (e.g. see Meidner & Mansfield, 1968). In other words, the stomata were thought to regulate gas exchange by processes of feedback, responding to plant internal variables which are themselves influenced by the magnitude of leaf conductance. There is no doubt that feedback of this type occurs and may in some circumstances be sufficient to explain a diurnal course of stomatal behaviour not, at first sight, dissimilar to that shown in Fig. 11. The stomata open in the morning and close in the evening in response to the decrease and increase in intercellular CO_2 concentration engendered by a change in rate of assimilation with change in light intensity. This suggestion was first made by Scarth (1932) and is on the whole strongly supported by the available evidence (see Raschke, 1975a).

The tendency for stomata sometimes to close about midday when the potential rate of transpiration is greatest has frequently been ascribed to decrease in leaf water potential associated with increase in actual rate of transpiration. Whether the influence of water potential on the guard cells is primarily a hydro-mechanical effect, or, as now appears to be the case, a synthesis of, and response to, abscisic acid and abscisic acid-like compounds is involved is irrelevant to this particular discussion. Sometimes midday closure of stomata has been attributed to enhanced intercellular CO_2 concentration resulting from increased respiration associated with increased temperature.

But feedback processes have certain limitations. If stomata open in the light as a result of a response to decrease in intercellular concentration of CO_2 rather than a direct response to light intensity, then intercellular CO_2 concentration must always diminish with increase in light intensity and *vice versa*. Similarly, if stomata close with increase in potential rate of transpiration as a result of a response to an internal factor associated with actual rate of transpiration rather than a response to the external factors which influence rate of transpiration, then the actual rate of transpiration must always increase with increase in potential rate of transpiration and *vice versa*.*

But in some circumstances, optimisation will demand that c_l increase with light intensity and that E decrease with increase in potential rate of transpiration. This is illustrated in Fig. 11, in which the variation in c_l and E is such that the variation in leaf conductance could not be achieved by the action of feedback alone. Of course our argument is incomplete, for it presumes that the responses of leaf conductance are quasi-steady. It is likely that the complex dynamic properties inherent in the feedback loops involving plant water relations and intercellular CO_2 are attuned to climate in such a way as to engender a degree of optimisation. However, these properties could only contribute to optimisation to the extent that the diurnal time course of climate is systematic; they could not (any more than could an endogenous rhythm in stomatal aperture) provide the basis of

* If the absolute gain of the feedback loop were infinite, as it is in an integral control system, then the stomata would just succeed in restoring rate of transpiration to its initial magnitude. If the absolute gain of the feedback loop involving c_l were infinite then the stomata would just succeed in restoring c_l to its initial magnitude. But neither is likely, because if the gain of either loop were infinite the other loop would be made ineffective. D. Dubbe, Farquhar & K. Raschke (unpublished data) have measured the gain of the CO_2 -feedback loop in several species in which stomata had been sensitised to CO_2 by application of abscisic acid (see Raschke, 1975b). The absolute gain, G , was in all cases less than 4; that is to say changes in c_l were always more than $1/(1+G) = \frac{1}{5}$ of what they would have been if the stomata were insensitive to CO_2 .

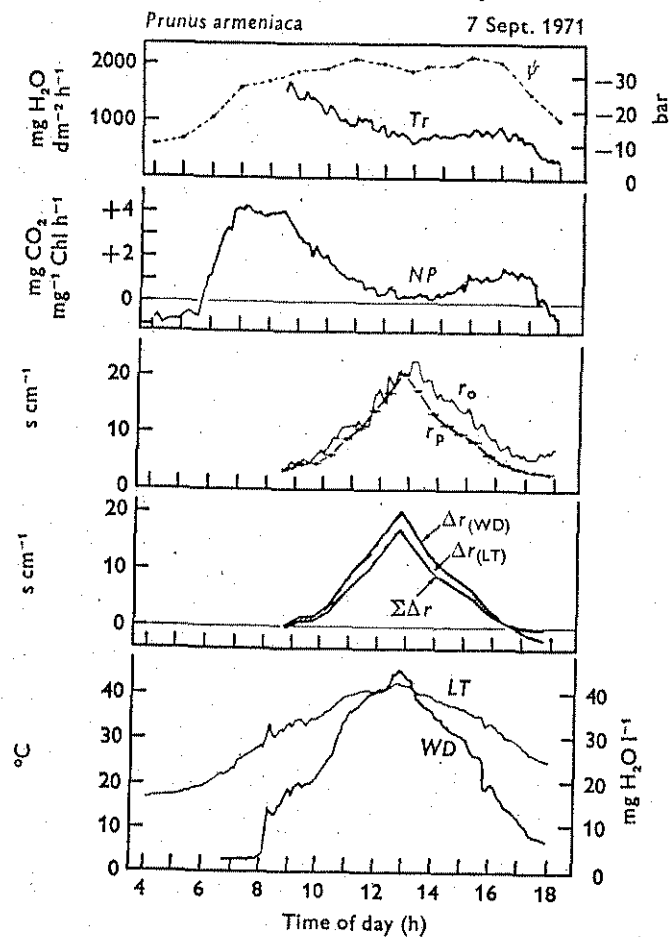


Fig. 12. Diurnal course in *Prunus armeniaca* of the negative hydrostatic pressure in the xylem (ψ), transpiration (Tr), net photosynthesis (NP), observed values of total diffusion resistance (r_0), predicted values of total diffusion resistance (r_p), change in diffusion resistance caused by changes in the water-vapour concentration difference between the leaf and the surrounding air ($\Delta r_{(WD)}$), change in diffusion resistance caused by changes in leaf temperature ($\Delta r_{(LT)}$), total change in diffusion resistance caused by changes in leaf temperature and water-vapour concentration difference ($\Sigma \Delta r$), leaf temperature (LT), and water-vapour concentration difference between the leaf and the surrounding air (WD). (Lange *et al.*, 1975.)

optimisation of stomatal response to stochastic changes in environment. And, with reference to Fig. 11, it would not be possible to explain both the increase in leaf conductance in the morning and the decrease in the evening on the basis of variation in c_1 ; nor is it likely that the prolonged midday depression, accompanied by decrease in both E and c_1 could be explained as a transient closure associated with early morning increase in E .

If feedback control cannot, in some circumstances at least, provide

optimal control then what are the alternatives? The most obvious one is that the stomata should be directly and suitably sensitive to certain characteristics of the external environment, such as light intensity, temperature and humidity. Schulze *et al.* (1972, 1974, 1975*a, b*) – see also Lange *et al.* (1975) – working with wild and cultivated plants in the Negev desert have advanced our knowledge of the way in which stomata can respond directly to the external conditions which affect transpiration rate. Fig. 12 shows the diurnal time course of leaf water potential, rate of transpiration, rate of assimilation, and total diffusive resistance to water vapour ($r_1 + r_b$ in our symbols) in *Prunus armeniaca*. The cause of the 'midday' closure of the stomata which commonly occurs in this species has been extensively investigated by Schulze, Lange, and their co-workers. It is not attributable to changes in leaf water status or intercellular CO_2 concentration (Schulze *et al.*, 1975*a*), or leaf temperature (Schulze *et al.*, 1975*b*). It appears to be a response to the difference in humidity, $w_1 - w_a$, between the leaf and the ambient atmosphere (Schulze *et al.*, 1972). Fig. 13 illustrates the change in total resistance, rate of transpiration, leaf water content, and rate of assimilation in *P. armeniaca* resulting from changes in the absolute humidity of the ambient air with leaf temperature maintained constant. Similar results were obtained with *Hammada scoparia* and *Zygo-phyllum dumosum*. Leaf temperature, as such, had a significant, but relatively small effect on total resistance provided the humidity difference was maintained constant. The sense of the temperature effect was different in different species. Hall & Kaufmann (1975) have obtained similar results with sesame, sunflower and sugar beet. In *P. armeniaca*, total resistance increased almost linearly with increase in $w_1 - w_a$ the slope being different at different times of the year (Fig. 14). Hall & Kaufmann found that the slope of the relationship progressively increased at large values of $w_1 - w_a$.

If we simulate the kind of experiment illustrated in Fig. 13, using the Hall-Björkman model of assimilation, and assuming that the stomata will maintain $\partial E / \partial A$ constant, we obtain results entirely consistent with the observations described. Fig. 15 shows the results of the simulation, light intensity being taken as $2 \text{ mEinstein m}^{-2} \text{ s}^{-1}$ and leaf temperature as 35°C . At the larger magnitudes of $\partial E / \partial A$ increase in leaf resistance with increase in $w_1 - w_a$ is small. Because rate of evaporation also increases, the optimal stomatal movement could be achieved on the basis of a feedback response alone. But at smaller magnitudes of $\partial E / \partial A$ the closure of the stomata with increase in $w_1 - w_a$ is so great that rate of transpiration is caused to decrease. We see, therefore, that whether or not feedback control can be sufficient to facilitate optimisation depends not only on metabolism and climate but also on the magnitude of $\partial E / \partial A = \lambda$.

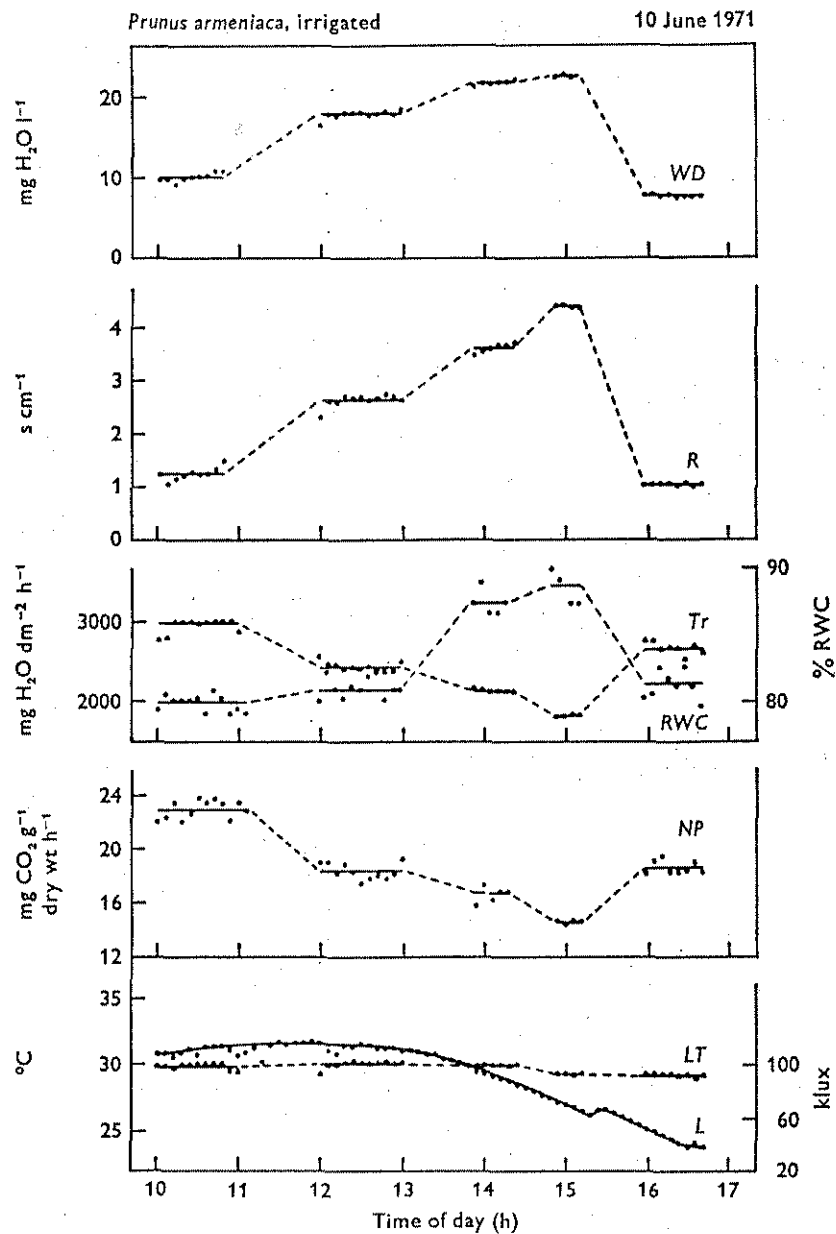


Fig. 13. Changes in the water-vapour concentration difference between the leaf and the surrounding air (WD), together with the changes in the total diffusion resistance (R), transpiration (Tr), net photosynthesis (NP), and relative water content (RWC) of the leaves in the irrigated *Prunus armeniaca*. The leaf temperature (LT) is kept constant. The light conditions (L) are natural. (After Schulze *et al.*, 1972.)

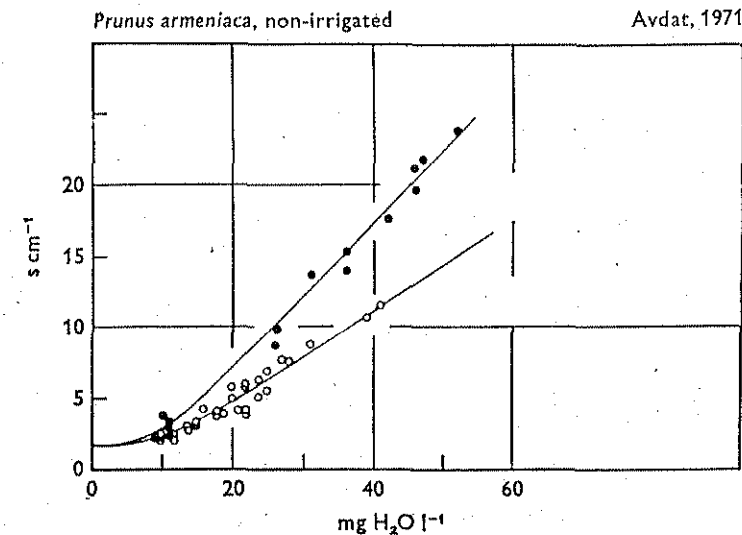


Fig. 14. The change of the total diffusion resistance ($s\text{ cm}^{-1}$) in *Prunus armeniaca* as related to the difference in water vapour concentration between the evaporating sites in the leaf and the air ($\text{mg H}_2\text{O l}^{-1}$) for May (\circ) and August (\bullet) 1971. The dots indicate the measured points of diffusion resistance during experiments with a variable water vapour difference but at a constant leaf temperature and at light saturation of net photosynthesis. (From Schulze *et al.*, 1974.)

Fig. 16 shows the results of a second simulated 'experiment'. Irradiance is varied while leaf temperature and ambient humidity are maintained constant at $20\text{ }^\circ\text{C}$ and 10^{-3} , respectively. At all magnitudes of $\partial E/\partial A$ the shape of the variation in intercellular CO_2 concentration is the same; c_1 diminishes as irradiance increases from the light compensation value up to 0.1 to $0.2\text{ mEinstein m}^2\text{ s}^{-1}$. Thereafter c_1 increases with increase in light intensity. This could occur only if stomata were directly sensitive to light. We know of no observations which support this prediction. That stomata do respond directly to light has been shown using epidermal strips in CO_2 -free air (Fischer, 1968). Also, differences in the action spectra for stomatal opening and rate of assimilation in intact leaves indicate that light-stimulated change in aperture cannot be accounted for by changes in intercellular CO_2 concentration alone. However, some authorities hold that direct responses to light are generally small (Raschke, 1975a). Whether they may be sufficient in particular species in particular circumstances to cause c_1 to increase with increase in light intensity is a matter for further investigation.

If stomata exhibit responses to a number of factors which influence – or are correlated with other factors which influence – $\partial E/\partial A$, with the effect

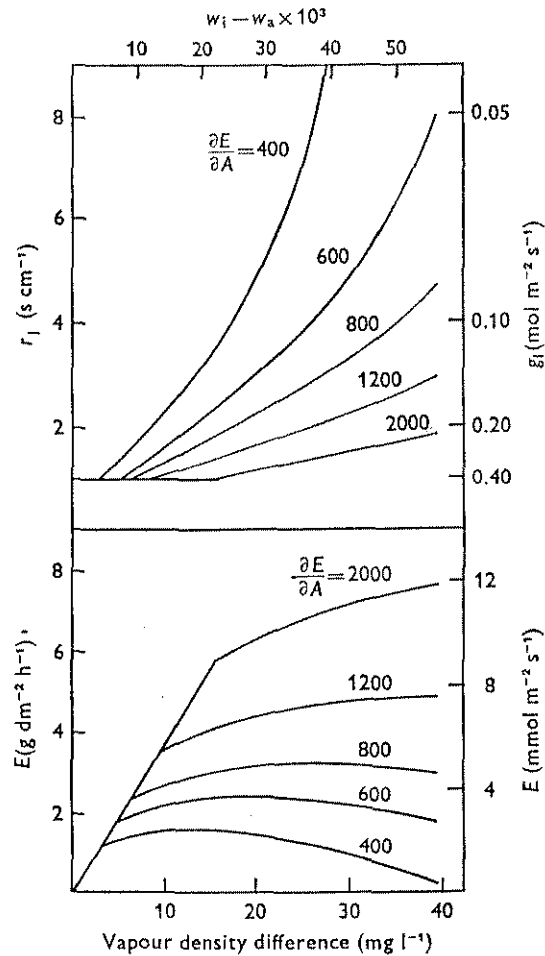


Fig. 15. Optimal resistance, r_1 , and rate of evaporation, E , as functions of humidity difference between leaf and air with leaf temperature and light intensity constant at 35°C and $2\text{ mEinstein m}^{-2}\text{ s}^{-1}$, respectively, for various magnitudes of $\partial E/\partial A$. Leaf metabolic characteristics taken to be those illustrated in Figs. 1 and 2.

that $\partial E/\partial A$ in fact tends to be maintained constant, then this constitutes 'inferred' sensing and control of $\partial E/\partial A$. We have discussed some responses, both feedback and feedforward, which might contribute to control by inference. To the extent that stomatal control of gas exchange depends on individually adapted responses of this kind, it is unlikely that a plant will exhibit optimisation in short-term experiments under artificial conditions. Only if great care were taken to mimic natural aerial and soil environments would $\partial E/\partial A = \lambda$ be observed in the laboratory. Indeed, optimisation

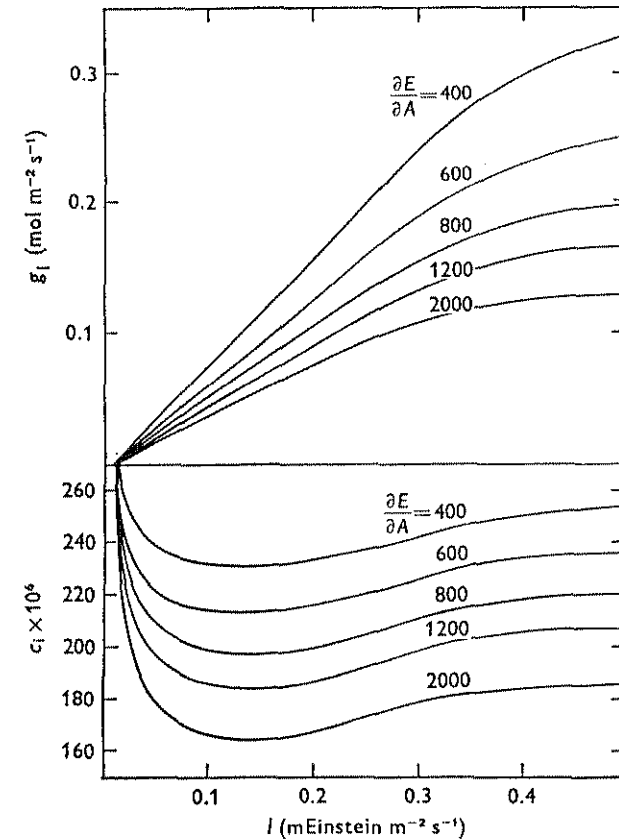


Fig. 16. Optimal leaf conductance, g_1 , and corresponding intercellular CO_2 concentration, c_i , as functions of irradiance, I , with leaf temperature and ambient humidity constant at 35°C and 10^{-3} , respectively, for various magnitudes of $\partial E/\partial A$. Leaf metabolic characteristics taken to be those illustrated in Figs. 1 and 2.

considered normal if plants have developed the means to sense the quantity $\partial E/\partial A$ itself, and to maintain that constant. This would be 'explicit', as contrasted to inferred, sensing and control. It is not entirely inconceivable that stomata could operate in this way; that the plant may determine $\partial E/\partial A$ dynamically by means of endogenous fluctuations in stomatal aperture at a frequency not strongly present in the frequency spectrum of environmental fluctuations, and adjust the mean level of stomatal aperture so that $\partial E/\partial A$ remains constant. Cowan (1972b) has discussed the possible role of stomatal oscillations in that context. Farquhar (1973) noted that the sampling theorem of information theory indicates that the system could only optimise at frequencies lower than the oscillation frequency. Environmental fluctuations at this and higher frequencies would constitute noise. However, while the notion of direct sensing and control is an appealing

one, there is a compelling piece of evidence which suggests that stomata do not operate in this way. It is shown in Appendix II that optimisation based on explicit sensing would sometimes require that stomata in illuminated leaves should open with increase in ambient concentration of CO_2 . We know of no evidence that they do; indeed they usually tend to close (see Meidner & Mansfield, 1968; Raschke, 1975a). It seems that stomata do not 'recognise' that an increase in c_1 resulting from an increase in c_a provides an enhanced opportunity to still further increase rate of assimilation but infer, instead, that it is caused by a decrease in the capability of the mesophyll to take up CO_2 - as in natural conditions it would be.

The arguments outlined in this section, and dealt with more rigorously in Appendix II, indicate an approach to the problem of relating specific facets of stomatal functioning to the characteristics of leaf metabolism and the environment for which a plant is adapted. We conclude with two other matters which may be germane to the co-evolution of stomatal and leaf metabolic characteristics.

MAXIMUM LEAF CONDUCTANCE

At large magnitudes of $\partial E/\partial A = \lambda$ the optimal time course of leaf conductance becomes almost identical with constant leaf conductance. It

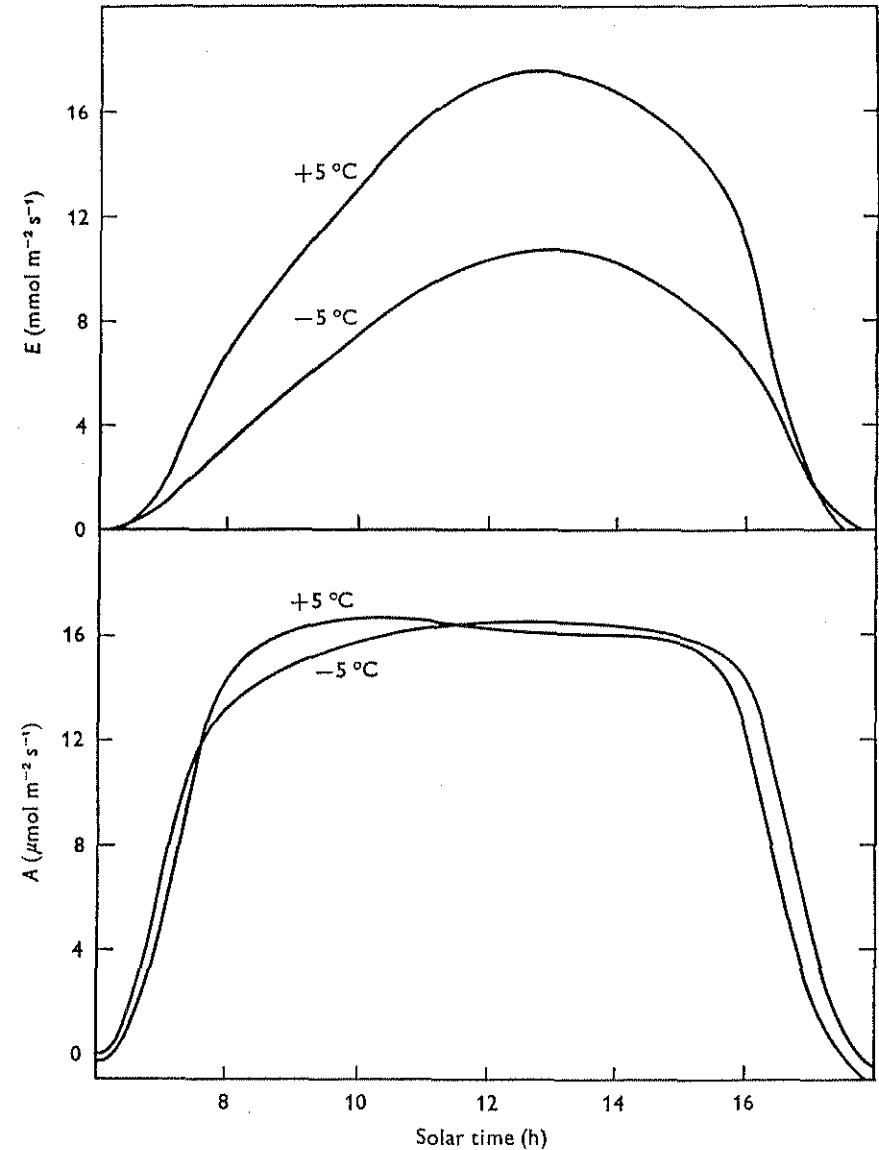
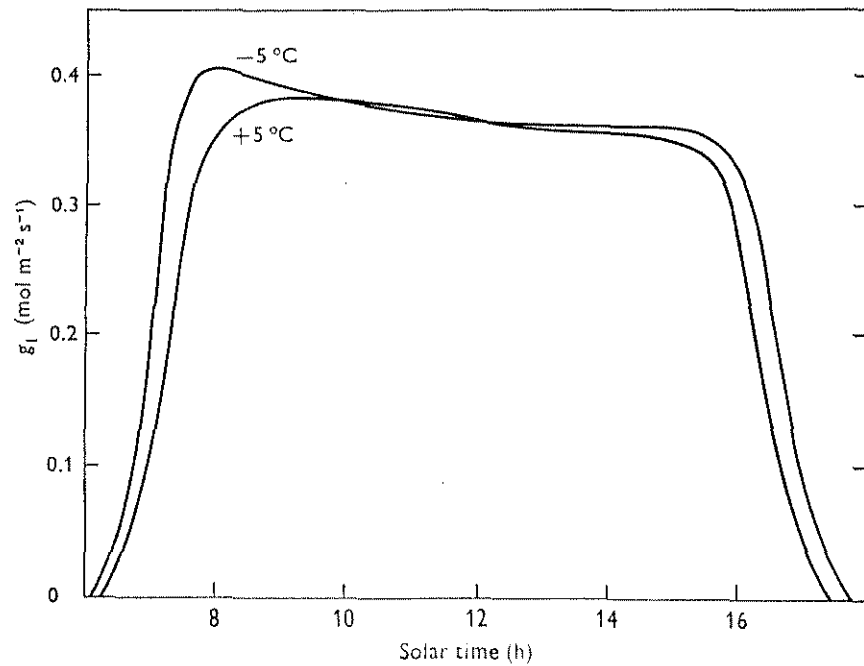


Fig. 17. As Fig. 8, but with $\lambda = 2000$.
 E = rate of evaporation; A = rate of assimilation.

is demonstrated by the comparison of \bar{E}/\bar{A} for optimal and constant leaf conductance in Fig. 7, and is further illustrated in Fig. 17. This figure is the counterpart of Fig. 8, but with $\lambda = 2000$ rather than 600. It is of interest that leaf conductance is almost constant throughout most of the day, and that it is very insensitive to changes in the mean level of temperature.

It is only in the region of this particular magnitude of λ that this lack of sensitivity occurs, and it is intriguing that it corresponds to a leaf conductance which is close to what is generally thought to be the maximum which occurs in C_3 plants, $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$ or, in conventional units, 1 cm s^{-1} . That this is so is because of a combination of circumstances which is perhaps best thought of as fortuitous. Nevertheless it serves to illustrate that optimal stomatal behaviour is not inconsistent with constant leaf conductance, and provokes the thought that the evolution of the metabolic characteristics of leaves may have taken place in such a way that maximum leaf conductance corresponds closely to an optimal leaf conductance which is rather insensitive to normal variations in environment and is associated with a rate of assimilation which, as in Fig. 17, is also insensitive to environment. In terms of the return from investment in the biochemical machinery of carbon fixation, there are obvious advantages in arranging that optimisation should correspond to a constant rate of assimilation.

INSTABILITY IN OPTIMISATION

In certain circumstances it is probable that regions of the $E = E(A, t)$ surface, in contrast to the example shown in Fig. 5, have a negative curvature $\partial^2 E / \partial A^2$. It is evident from an examination of equation (7) that $\partial E / \partial A$ constant within such a region defines not the minimum, but the maximum possible loss of water corresponding to a given amount of assimilation. A region in which $\partial^2 E / \partial A^2$ is negative is a region of instability in terms of optimal stomatal behaviour, for the ratio E/A is decreased by increase in leaf conductance. It may be shown that leaf conductance at any given instant of time must either be zero or be sufficiently great for A and E to exceed the magnitudes corresponding to the point of inflexion at which the curvature of the surface becomes positive. There are three factors which tend to cause a 'bump' in the $E(A, t)$ surface. If the boundary layer conductance is very small, as with large leaves or small windspeed, leaf temperature will greatly exceed ambient temperature when the stomata are nearly closed, and will diminish considerably with increase of leaf conductance resulting from evaporative cooling. The effect is that rate of evaporation increases relatively less rapidly with increase in conductance than in leaves having a large boundary layer conductance. An example of the influence of boundary layer conductance on optimal leaf conductance is illustrated in Fig. 18. When boundary layer conductance is taken to be twice that depicted in Fig. 4 there is very little effect on optimal behaviour; but, when it is halved, leaf conductance avoids a small region in the

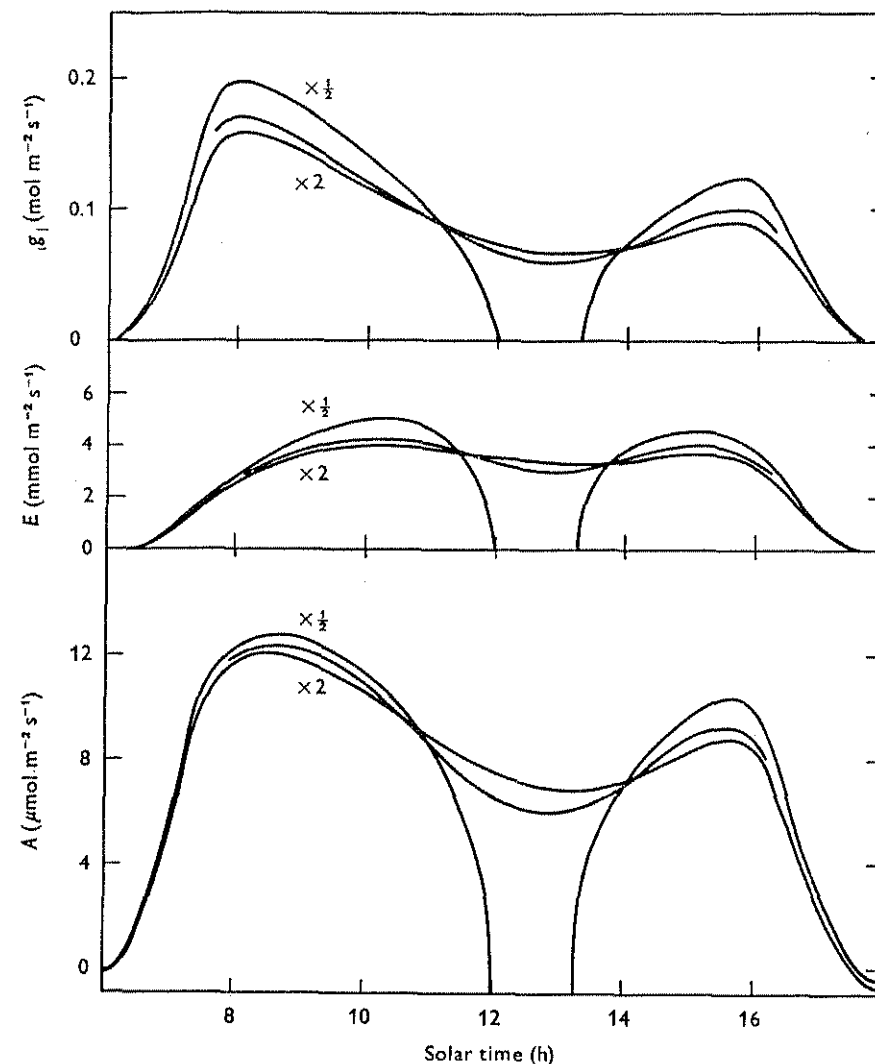


Fig. 18. Optimal rate of assimilation, A , rate of evaporation, E , and leaf conductance, g_b , for $\lambda = 600$. The truncated curves pertain to the metabolic and climatic characteristics on which Fig. 5 is based. The other curves pertain to the same characteristics, except that boundary layer conductance is taken to be twice as great in one case ($\times 2$) and half as great in the other ($\times \frac{1}{2}$).

$E = E(A, t)$ surface which develops a negative curvature by going rapidly to zero. The tendency for instability of this kind to develop is enhanced if air temperature is high, for then change in the CO_2 compensation point Γ with change in leaf temperature is such that rate of assimilation may increase relatively very rapidly with increase in leaf conductance. We would expect plants which have evolved large leaves in hot climates to be

those which are normally able to operate at large magnitudes of $\partial E/\partial A$ and thus avoid stomatal closure of the kind illustrated in Fig. 18. The third factor which strongly influences the curvature of the $E(A,t)$ surface is the so-called 'internal resistance' to CO_2 uptake. If this is small then rate of assimilation may be relatively more sensitive to change in leaf conductance than is rate of evaporation. The tendency for the variance in optimal leaf conductance to be greater the smaller the internal resistance is illustrated in Fig. 9. With those C_4 species in which the internal resistance is an order of magnitude less than that in C_3 species, $\partial^2 E/\partial A^2$ is likely to be negative in a wide range of climatic conditions and over a wide range of leaf conductance. This suggests that there might be marked differences in the nature of stomatal functioning in these species, compared with those in which the carboxylating system has a smaller affinity for CO_2 .

DISCUSSION

In the short term, stomata appear to regulate gas exchange. But on an evolutionary time scale, and in a particular sense, they probably have had very little influence on the form and function of higher plants. All higher plants evidently developed stomata very early, and it is doubtful whether the need to have stomata with particular characteristics suited to particular environments has offered any substantial subsequent impediment to plant adaptation. It seems unlikely, for example, that the requirement that stomata should sometimes open in the dark and close in the light would have appreciably retarded the divergence of plants having Crassulacean acid metabolism. In other words we would expect that stomatal characteristics would adhere at all times rather closely to those characteristics most suited to the success of a particular species. This is the view that we have taken here; the main constraint that the characteristics of the epidermis impose on the functioning of the plant is summed up by the observation that water vapour will pass about 1.6 times more readily through the stomatal pore than will CO_2 . Of course, in an environment different from that in which a particular species has evolved, it may be that the characteristics of stomata and stomatal behaviour are not always those most appropriate to plant survival. Even so, it is possible that stomata have a greater ability to behave appropriately in widely differing circumstances than does the plant as a whole – we note that the stomata in *Prunus armeniaca* appear to function efficiently in the Negev desert though the species is not well adapted to that environment. It follows from this view, that the problem of understanding stomatal behaviour may be one not so much of unravelling the mechanics of the guard cell and their inter-relationships

with the mechanics of the leaf, but one of being able to formulate, in a way which combines ecological and physiological considerations, the metabolic requirements of a plant in terms of gas exchange. It may be that our hypothesis is incorrect; it is almost certainly a restricted expression of the truth at best. But we suspect that the exploration of hypotheses of this kind affords the most likely means of 'integrating' activity of stomata with that of the plant as a whole.

We are grateful to Professors O. L. Lange and E.-D. Schulze for helpful discussion. One of us, I. R. C., is indebted both to the Lehrstuhl Pflanzenökologie, University of Bayreuth, and the Botanisches Institut, University of Würzburg, for hospitality, and to the former for financial support, while this work was carried out.

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APPENDIX I

Determination of $\partial E/\partial A$

It is necessary to find the sensitivities of E and A to change in leaf conductance and make use of the identity

$$\frac{\partial E}{\partial A} = \frac{\partial E/\partial g_1}{\partial A/\partial g_1} \quad (14)$$

The quantity $\partial E/\partial g_1$, which has been shown by Farquhar & Cowan (1974) to play an important role in the dynamic behaviour of stomata, may be expressed, by differentiating equations (4) with respect to r_1 and eliminating $\partial T_1/\partial r_1$, as

$$\frac{\partial E}{\partial g_1} = -r_1^2 \frac{\partial E}{\partial r_1} = \frac{r_1^2 E}{r_1 + r_b + r_b^* \frac{L}{C_p} \frac{dw'}{dT_1}}, \quad (15)$$

where

$$r_b^* = \frac{1.12 r_b}{1 + 9r_b \sigma T_1^3 / C_p} \quad (16)$$

is the effective boundary layer resistance to transfer of sensible heat and thermal radiation. All the variable terms in these expressions are obtained in the standard procedure for finding r_1 in gas exchange experiments. The

main impediment to the determination of $\partial E/\partial A$ rests with the other component, $\partial A/\partial g_1$. Differentiating equations (5) with respect to r_1 , eliminating $\partial c_1/\partial r_1$ and making use of the second of equations (4), it may be shown that

$$\frac{\partial A}{\partial g_1} = -r_1^2 \frac{\partial A}{\partial r_1} = \frac{1.6r_1^2 A \frac{L}{C_p} \frac{\partial A/\partial T_1}{\partial A/\partial c_1} \frac{\partial E}{\partial g_1}}{1.35r_b + 1.6r_1 + 1/(\partial A/\partial c_1)} \quad (17)$$

It is implicit that $\partial A/\partial T_1$ is at constant c_1 and I , and $\partial A/\partial c_1$ at constant T_1 and I . These two metabolic characteristics are not normally measured during observations of gas exchange in the field. To find the function $A(c_1, T_1, I)$, even within the limited region relating to the normal functioning of a plant, requires a quite demanding and time-consuming subsidiary experiment. Perhaps an alternative is to attempt to determine the differentials during observations of the normal activity of a plant by superimposing small periodic fluctuations in CO_2 concentration and temperature on the ambient environment and relating the resulting perturbations in A to those in c_1 and T_1 .

APPENDIX II

Optimisation and the limitations of feedback

Let there be an external environmental variable, x say, which changes with time and tends to cause $\partial E/\partial A$ to change. If leaf conductance is to adjust in such a way as to maintain $\partial E/\partial A = \lambda$ constant, then

$$\left(\frac{\partial \lambda}{\partial x}\right)_{g_1} \frac{dx}{dt} + \left(\frac{\partial \lambda}{\partial g_1}\right)_t \frac{dg_1}{dt} = 0. \quad (18)$$

Let there also be an internal physiological variable, x_1 , which is caused to change by change in x and is defined so that it changes in the same sense as x . Thus if $x = I$, then we might have $x_1 = -c_1$.

Then

$$\frac{dx_1}{dt} = \left(\frac{\partial x_1}{\partial x}\right)_{g_1} \frac{dx}{dt} + \left(\frac{\partial x_1}{\partial g_1}\right)_t \frac{dg_1}{dt}. \quad (19)$$

Eliminating dg_1/dt from equations (18) and (19) it follows that

$$\frac{dx_1}{dx} = \left(\frac{\partial x_1}{\partial x}\right)_{g_1} - \frac{\left(\frac{\partial x_1}{\partial g_1}\right)_t \left(\frac{\partial \lambda}{\partial x}\right)_{g_1}}{\left(\frac{\partial \lambda}{\partial g_1}\right)_t}. \quad (20)$$

If the stomata respond to x_1 rather than x directly, and if $(\partial x_1/\partial g_1)_t$ is

finite, then x_1 and g_1 are elements in a feedback loop. Therefore dx_1/dx must be positive and hence

$$\left(\frac{\partial x_1}{\partial g_1}\right)_t \left(\frac{\partial \lambda}{\partial x}\right)_{g_1} < \left(\frac{\partial x_1}{\partial x}\right)_{g_1} \left(\frac{\partial \lambda}{\partial g_1}\right)_t, \quad (21)$$

in which we have been able to multiply throughout by $(\partial \lambda / \partial g_1)_t$ because this term is positive.

Equation (21) determines whether or not a particular feedback loop involving x_1 is capable of optimising stomatal behaviour when the gas exchange system is perturbed by a change in x . However, the use of the criterion in conjunction with equations (4) and (5) involves tedious algebra and leads to somewhat complex results. For the purposes of illustration we use a simplified description of the processes of gas exchange, based on the assumption that boundary layer resistance is negligible. Equations (4) and (5) become

$$E = (w'(T_a) - w_a) \cdot g_1 \quad (22)$$

and

$$A = (c_a - c_i) \cdot g_1 / 1.6 = A(c_i, T_a, I), \quad (23)$$

and equations (15) and (17) are also much abbreviated.

First let us take $x = I$ and $x_1 = -c_i$. Then it may be shown that equation (21) leads to

$$\frac{\partial}{\partial I} \left(\frac{I}{A} \frac{\partial A}{\partial c_i} \right) < 0. \quad (24)$$

The condition may be given a geometric interpretation. If we draw a tangent to one of the characteristics in Fig. 1 and define the point at which it intercepts the c_i axis as c_0 , then equation (24) implies

$$\left(\frac{\partial c_0}{\partial I}\right)_{c_i} < 0. \quad (25)$$

Only when c_i , T_a , and I are such that this condition is met can stomata respond optimally to a change in I by virtue of their sensitivity to c_i alone. It may readily be verified that the condition is not fulfilled in Fig. 1 if I is greater than about $200 \mu\text{Einstein m}^{-2} \text{s}^{-1}$. The same conclusion applies at other temperatures also, as Fig. 16 indicates.

Now put $x = w_a$ and $x_1 = -E$. Equation (21) leads to

$$\frac{\partial}{\partial A} \left(\frac{\lambda}{E} \right) > 0. \quad (26)$$

This condition can also be given a simple geometric interpretation. If we draw a tangent to the curve E as a function of A (environment being

constant), and define the point at which it intercepts the $A = 0$ axis as A_0 then equation (26) implies that

$$\frac{\partial A_0}{\partial A} > 1. \quad (27)$$

It may be shown that certain regions of the surface in Fig. 5 do not conform to the condition. We conclude that, insofar as we have been justified in neglecting the influence of boundary layer resistance, these regions define circumstances in which the stomata cannot respond optimally to change in ambient humidity by virtue of their sensitivity to plant internal water relations alone. Another example of the inadequacy of feedback is illustrated in Fig. 15. It is worth remarking that the inequality cannot in any circumstances be satisfied when $E = A = 0$; nor is it satisfied if the curvature $\partial \lambda / \partial A = \partial^2 A / \partial A^2$ is small.

Finally, we consider a slightly different problem. Equation (18) may be rewritten

$$\frac{dg_1}{dx} = \frac{\left(\frac{\partial \lambda}{\partial x}\right)_{g_1}}{\left(\frac{\partial \lambda}{\partial g_1}\right)_t}. \quad (28)$$

As $(\partial \lambda / \partial g_1)_t$ is positive, the sign of dg_1/dx is determined by that of the other partial differential. If we take $x = c_a$ it may be shown that dg_1/dc_a is positive if

$$\left(\frac{\partial A}{\partial c_i}\right)^2 \left[1 + \frac{1.6(\partial A / \partial c_i)}{g_1} \right] + A \frac{\partial^2 A}{\partial c_i^2} > 0. \quad (29)$$

The quantity $\partial^2 A / \partial c_i^2$ is negative, but clearly the condition is fulfilled if c_i , and therefore A , is small. Then optimisation requires that stomata open with increase in c_a . The conclusion is relevant to our discussion of 'inferred' and 'explicit' sensing and control.