

STOMATAL DYNAMICS IN THE LEAVES OF GREEN PLANTS

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ABSTRACT

Stomata are microscopic pores in the leaves of green plants through which gas exchange occurs. The stomatal pore may be open or closed depending upon the hydrostatic pressure in specialized guard cells, and thus stomata may act as valves to limit water vapor loss while permitting carbon dioxide to enter the leaf for use in photosynthesis.

This work presents a model of the dynamics of stomatal behavior. It is based on a balance of water fluxes between stomatal guard cells and the vascular system, and includes diffusion of water potential within the vascular tissue. Mathematically, the model consists of a partial differential equation coupled to a linear ordinary differential equation. The partial differential equation contains the only nonlinearity in the model, a ramp function of the dependent variable. The latter derives from the fact that all guard cell pressures which lead to a closed pore are equivalently effective, while in the case of an open pore, greater pressures lead to greater pore widths and greater water loss.

Analysis of the model is shown to support recent experimental evidence that stomatal opening occurs in organized spatial patterns across the surface of the leaf, i.e. in waves.

NOMENCLATURE

A = area of apoplasm-guard cell interface [cm^2]
 \tilde{A} = area of apoplasm pathway [cm^2]
 b = length of stomatal pore [cm]
 c_0 = guard cell elastostatic constant [cm]
 c_1 = guard cell elastostatic constant [cm/bar]
 d = distance between neighboring stomata [cm]
 E = elastic modulus of the guard cell wall [bar]
 f = water potential mode shape, eq.(33)
 g = guard cell pressure mode shape, eq.(34)
 $H(\cdot)$ = the Heaviside step function
 J = flux of water into guard cell [$\text{cm}^3/\text{cm}^2\text{-sec}$]

\tilde{J} = evaporative flux of water vapor [$\text{cm}^3/\text{cm}^2\text{-sec}$]
 ℓ = dimensionless leaf half-width, eq.(19)
 L = hydraulic conductivity of guard cell wall [$\text{cm}/\text{sec-bar}$]
 \tilde{L} = hydraulic conductivity of the apoplasm [$\text{cm}/\text{sec-bar}$]
 p = hydrostatic pressure in guard cell [bar]
 r = characteristic exponent, eq.(33)
 S = apoplasmic storage coefficient [$\text{cm}^3/\text{cm}^3\text{-bar}$]
 t = time [sec]
 u = transformed guard cell pressure [bar], eq.(12)
 \hat{u} = steady state pressure field [bar]
 U = small perturbation from steady state pressure [bar]
 V = guard cell volume [cm^3]
 V^0 = guard cell volume at incipient plasmolysis [cm^3]
 \tilde{V} = control volume of apoplasm near stomatal pore [cm^3]
 w = width of stomatal pore [cm]
 x = distance across leaf from midrib to leaf edge [cm]
 z = transformed leaf water potential [bar], eq.(13)
 z_0 = transformed petiole water potential [bar], eq.(18)
 \hat{z} = steady state water potential field [bar]
 Z = small perturbation from steady state water potential [bar]
 α = dimensionless constant, eq.(16)
 β = dimensionless constant, eq.(17)
 λ = half-width of the leaf [cm]
 ξ = dimensionless distance across leaf, eq.(15)
 π = osmotic pressure in guard cell [bar]
 π^0 = osmotic pressure in guard cell at incipient plasmolysis [bar]
 τ = dimensionless time, eq.(14)
 ψ = leaf water potential [bar]
 ψ_0 = applied water potential at the petiole [bar]
 $\omega = \sqrt{\alpha/\beta}$, eq.(22)

INTRODUCTION

The motivation for studying the dynamics of leaves is that leaves play the essential role of capturing solar energy for the production of fruits, vegetables, nuts and other forms of food, to be eaten directly by our species, or by other species in the food chain.

Photosynthesis is the process by which the sun's rays are converted into stored chemical energy. It requires CO_2 , water and sunlight, and produces glucose (a simple sugar) and oxygen.

Photosynthesis occurs in the chloroplasts of mesophyll cells in the interior of leaves. The required CO_2 enters the leaf through small holes in the leaf surface called stomata (Fig.1), while the required water is brought to the leaf from the soil by the plant's vascular xylem tissue.

The open stomatal pores offer an entrance or exit to any gases present. The flow of such gases is diffusive, driven by differences in concentration between the leaf interior and the ambient atmosphere. In particular, water vapor, present in the nearly 100% relative humidity of the intercellular air spaces of the leaf, will be lost through the stomatal pores. If water so lost is not able to be replaced quickly enough, e.g. in times of drought when the soil lacks moisture, then disastrous consequences for the plant may ensue. On the scale of an individual plant cell, the progressive loss of water will eventually cause the cell membrane to shrink and rip away from the relatively rigid cell wall, a condition called plasmolysis. On the scale of the whole plant this appears as wilting.

Nature has designed the stomatal pore system so as to save as much water as possible from being lost to the environment. This is accomplished by permitting the stomatal pores to vary their sizes in response to environmental factors. An individual stomate consists of a pair of guard cells which surround the stomatal pore (Fig.2). The width of the pore can be controlled by the hydrostatic (or "turgor") pressure in the guard cells. For example, in the absence of sunlight, a complicated photosensitive feedback system is thought to adjust the concentration of solutes in the guard cell, which in turn affects the rate at which water enters the guard cell from the leaf vascular system, resulting in a loss of turgor pressure inside the guard cell and a closing of the stomatal pore. Thus stomata are generally closed at night, in order to conserve water when photosynthesis is impossible.

In this paper we shall be concerned with the dynamics of a field of stomata spread across the leaf surface. Experimental evidence has been previously presented [1,2] showing that these dynamics involve complicated time-varying spatial patterns, including waves moving across the leaf. We shall present a mathematical model of leaf dynamics, derived from fundamental conservation laws, in an effort to understand the mechanism of such waves.

The model will utilize a basic concept invented by plant physiologists to describe the relative state of moisture inside the plant, called water potential ψ [3]. Water flows due to a negative gradient in ψ , just as in thermodynamics heat flows due to a negative gradient in temperature. The model is based on the following two effects: (i) an open stomatal pore will be a sink for the loss of water vapor by evaporation, and thus will lower the local water potential, and (ii) an increase in availability of vascular water will increase the local guard cell hydrostatic pressure,

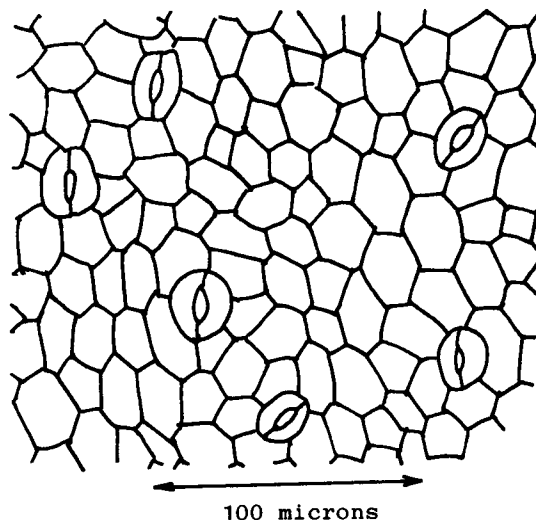


Fig.1. Stomatal pores on the leaf surface.

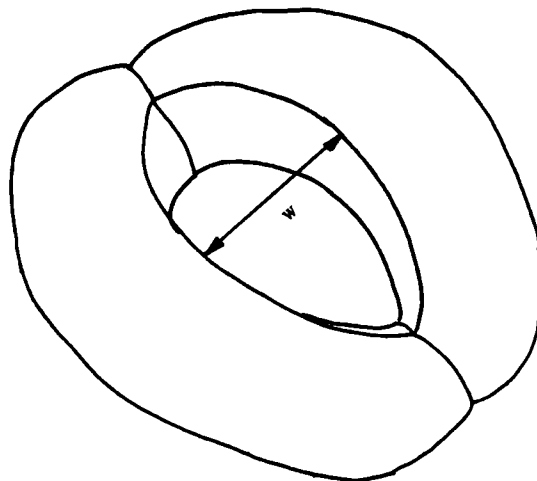


Fig.2. A pair of guard cells surrounding a stomatal pore. w = pore width.

thereby causing the stomatal pore to tend to open. In terms of the state variables of the model, water potential ψ and guard cell pressure p (both field quantities), these effects represent two-way coupling. That is, (i) the value of p determines the pore width w which affects the local value of ψ , and (ii) the value of ψ determines the local availability of water which affects p . When expressed mathematically, these statements represent coupling terms in the differential equations on the dynamics of the ψ and p fields.

LITERATURE REVIEW

The work presented in this paper is part of a series of works involving the mathematical modeling of leaves. Since the present model is strongly based upon this previous research, the following brief literature review is presented.

The statics of the guard cell were studied by using finite element analysis [4,5]. It was found that an increase in the hydrostatic pressure inside the guard cell caused the stomatal pore to open.

The gaseous diffusion of water vapor and CO_2 in the leaf were studied by a variety of methods [6-9]. It was found that water vapor evaporated from the immediate neighborhood of the stomatal pore while CO_2 diffused effectively to the deep interior of the leaf. It was shown that a pore that was open only slightly, could be nearly as effective in diffusing gas as a wide-open pore, if the ambient still-air boundary layer was sufficiently large (i.e., if the wind was small.)

In the case of CO_2 , the gaseous diffusion problem is related to the diffusion of CO_2 as a solute into the interior of the mesophyll cells where it is utilized in photosynthesis [10]. By combining these pathways, a comprehensive model of CO_2 diffusion was presented [11].

In the case of water flow in the leaf, we took account of the xylem pathway by which water is drawn up through the plant from the soil. The ultimate source of tension in the contiguous column of water reaching from the roots to the leaves are the microscopic menisci in the mesophyll cell walls [12]. The flow of water in the leaf was studied using partial differential equations in [13].

The foregoing work on stomatal statics and diffusion in the leaf was utilized in models of the dynamics of individual stomates [14-16]. It was shown that there were two modes of oscillation possible, one of about 20 minute period associated with a hydraulic feedback loop, and another of about 2 minute period associated with a CO_2 feedback loop. It was also noted that these oscillations (limit cycles) were relatively unusual, a result of Hopf and other bifurcations [17], and that an equilibrium steady state was more typical of the behavior of the single stomate models.

These stomate models were applied to questions of plant productivity, water-use efficiency and greenhouse crop production [18,19]. It was concluded that stomatal oscillations offer the plant a gradual transition between the fully open and fully closed pore states.

Most recently, we have extended the single stomate model to models of stomatal behavior involving the whole leaf [20,2]. These models are closely related to the present work. Both [20] and [2] involve modeling the dynamics of water potential propagation in the leaf by a diffusion equation with a sink for water lost through the stomatal pores via evaporation. However,

the treatment of the dynamics of the individual stomates in [20], [2] and the present work are quite different. In [20] we modeled the dynamics of the individual stomate only by reference to its phase. In [2] we used a more realistic model of the stomate, representing its dynamics by a flow on the guard cell-subidiary cell pressure plane, after previous models [14,17]. However, we offered no derivation of these dynamics, and simply chose the flow to correspond to a damped oscillator. The results showed that the model [2] displayed waves of stomatal opening, including a steady state periodic wave associated with a Hopf-like bifurcation. In contrast to [2], the present work models the stomate by a single dynamical variable, the guard cell pressure, and we provide a realistic derivation based on physical principles.

For a more comprehensive review of mathematical models of green plants, the reader is referred to [21].

DERIVATION OF MODEL

We model the dynamics of water transport in the leaf by assuming that water diffuses in the plane of the leaf through the apoplasm, i.e. the xylem tissue as well as the matrix of contiguous cell wall interstices. This flow affects the turgor of all living cells in the leaf, including the guard cells which influence the size of the stomatal pores. Water evaporating from the wet apoplasmic surfaces diffuses as water vapor through the intercellular air pathways and exits the leaf via the stomatal pores, if they are open. This evaporative flux lowers the water potential in the apoplasm near the stomatal pore, and thus open stomata act like a sink for the diffusion of water potential [20]:

$$(1) \quad \tilde{V} S \frac{\partial \psi}{\partial t} = \tilde{A} \tilde{L} d^2 \left[\frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right] - \tilde{J} b w$$

where $\psi = \psi(x,y,t)$ = leaf water potential [bar],

\tilde{V} = volume of apoplasm lying in the neighborhood of a single stomatal pore [cm^3],

S = apoplasmic storage coefficient [$\text{cm}^3/\text{cm}^3\text{-bar}$],

\tilde{A} = area of apoplasm pathway perpendicular to the direction of flow [cm^2],

\tilde{L} = hydraulic conductivity of the apoplasm [$\text{cm}/\text{sec-bar}$],

d = distance between neighboring stomata [cm],

\tilde{J} = flux of water from the apoplasm cell walls to the vapor phase [$\text{cm}^3/\text{cm}^2\text{-sec}$],

b = length of stomatal pore [cm],

$w = w(x,y,t)$ = width of stomatal pore [cm].

The model asserts that the pore width w is determined by the hydrostatic (or turgor) pressure p [bar] in the guard cell. On the basis of previous studies [4,9], we assume that

$$(2) \quad w = (c_1 p - c_0) H(c_1 p - c_0)$$

where c_0 [cm] and c_1 [cm/bar] are positive constants,

$H(\cdot)$ = the Heaviside step function.

Finally we model the effect of changes in apoplasmic water potential ψ on the dynamics of the guard cell pressure p [14,16]. Conservation of mass for water flow from the apoplasm to the guard cell requires that

$$(3) \quad \frac{\partial V}{\partial t} = J A$$

where V = guard cell volume [cm^3],

J = flux of water from apoplasm to guard cell [$\text{cm}^3/\text{cm}^2\text{-sec}$],

A = area of interface between apoplasm and guard cell [cm^2].

The flux J may be related to water potentials in the apoplasm and guard cell by the expression

$$(4) \quad J = L (\psi_{\text{ap}} - \psi_{\text{gc}})$$

where L = hydraulic conductivity [$\text{cm}^2/\text{sec-bar}$],

$\psi_{\text{ap}} = \psi$ = water potential in the apoplasm [bar],

$\psi_{\text{gc}} = p - \pi$ = water potential in the guard cell [bar],

p = hydrostatic pressure in guard cell [bar],

π = osmotic pressure in guard cell [bar].

The osmotic pressure π is proportional to the concentration of solutes inside the guard cell. Conservation of the solute mass requires that

$$(5) \quad \pi V = \pi^0 V^0$$

where superscripts correspond to incipient plasmolysis, i.e., the state of the guard cell in which the cell membrane exerts no pressure against the cell wall.

The guard cell is modeled as an elastic shell, and we assume that the volume change from the unstressed state is proportional to the internal pressure p :

$$(6) \quad p = E \left[\frac{V - V^0}{V^0} \right]$$

where E = elastic modulus of the guard cell wall [bar].

Now we differentiate (6) with respect to time t , then substitute eqs.(3) and (4) to obtain

$$(7) \quad \frac{\partial p}{\partial t} = \frac{L A E}{V^0} (\psi - p + \pi)$$

Solving (5) for π and expanding for small volume changes gives

$$(8) \quad \pi = \frac{\pi^0}{1 + \frac{V - V^0}{V^0}} \approx \pi^0 \left[1 - \left[\frac{V - V^0}{V^0} \right] \right] \approx \pi^0 \left[1 - \frac{p}{E} \right]$$

Substituting (8) into (7) gives

$$(9) \quad \frac{\partial p}{\partial t} = \frac{L A E}{V^0} \left(\psi - p \left[1 + \frac{\pi^0}{E} \right] + \pi^0 \right)$$

BOUNDARY CONDITIONS

For mathematical simplicity, we consider a one dimensional version of the model in which the field variables ψ and p depend on x and t only. We imagine the x direction to lie in the plane of the leaf perpendicular to the midrib. We assume the resistance to flow in the midrib to be relatively small so that the water potential along the length of the midrib is nearly equal to its value at the petiole. This leads

to the boundary condition

$$(10) \quad \psi = \psi_0, \quad x = 0$$

where ψ_0 [bar] is the applied water potential at the petiole.

At the leaf's edge we assume no flux in the plane of the leaf:

$$(11) \quad \frac{\partial \psi}{\partial x} = 0, \quad x = \lambda$$

where λ [cm] is the half-width of the leaf.

CHANGE OF VARIABLES

In order to simplify the handling of the model equations we introduce the following change of variables:

$$(12) \quad u = p - \frac{c_0}{c_1}$$

$$(13) \quad z = \psi + \pi^0 - \frac{c_0}{c_1} \left[1 + \frac{\pi^0}{E} \right]$$

$$(14) \quad \tau = \frac{L A}{V^0} (E + \pi^0) t$$

$$(15) \quad \xi = \left[\frac{L A \tilde{V} S}{\tilde{L} \tilde{A} V^0 d^2} (E + \pi^0) \right]^{1/2} x$$

whereupon the model equations (1),(2),(9)-(11) become

$$(16) \quad \frac{\partial z}{\partial \tau} = \frac{\partial^2 z}{\partial \xi^2} - \alpha u H(u)$$

$$(17) \quad \frac{\partial u}{\partial \tau} = -u + \beta z$$

$$(18) \quad z = z_0, \quad \xi = 0$$

$$(19) \quad \frac{\partial z}{\partial \xi} = 0, \quad \xi = \ell$$

where

$$\alpha = \frac{V^0 b \tilde{J} c_1}{\tilde{V} A L S (E + \pi^0)}$$

$$\beta = \frac{E}{E + \pi^0}$$

$$z_0 = \psi_0 + \pi^0 - \frac{c_0}{c_1} \left[1 + \frac{\pi^0}{E} \right]$$

$$\ell = \left[\frac{L A \tilde{V} S}{\tilde{L} \tilde{A} V^0 d^2} (E + \pi^0) \right]^{1/2} \lambda$$

The problem is to solve eqs.(16)-(19) for $u(\xi, \tau)$ and $z(\xi, \tau)$ for suitable initial conditions on u and z . The u variable represents both guard cell pressures and pore sizes, while the z variable represents leaf water potential. The model has three parameters, α , β , and ℓ . In addition, the water potential at the petiole $z_0 = z_0(\tau)$ is a prescribed function of time τ .

STEADY STATE SOLUTIONS

We look for steady state solutions to eqs.(16)-(19) in the two cases that (i) all pores are open, and (ii) all pores are closed. In order to achieve a time independent steady state, we assume the petiole potential z_0 is constant in time.

Case (i) If all pores are open, then $u > 0$ for all ξ , and at steady state eqs.(16) and (17) become:

$$(20) \quad 0 = \frac{d^2 \hat{z}}{d\xi^2} - \alpha \hat{u}$$

$$(21) \quad 0 = -\hat{u} + \beta \hat{z}$$

where $z = \hat{z}(\xi)$ and $u = \hat{u}(\xi)$ are the steady state water potential and guard cell pressure fields, respectively. Solving (21) for \hat{u} and substituting in (20), we obtain

$$(22) \quad 0 = \frac{d^2 \hat{z}}{d\xi^2} - \omega^2 \hat{z}$$

where $\omega^2 = \alpha \beta$. Solving (22) according to the boundary conditions (18) and (19) gives

$$(23) \quad \hat{z} = z_0 \frac{\cosh \omega(\ell - \xi)}{\cosh \omega \ell}, \quad \hat{u} = \beta z_0 \frac{\cosh \omega(\ell - \xi)}{\cosh \omega \ell}$$

Here the open pore assumption of $u > 0$ for all ξ requires, from (23), that $z_0 > 0$. Note that at steady state, stomata close to the water source at the midrib $\xi = 0$ are predicted to have higher water potentials, higher guard cell turgor pressures and larger pore widths than stomata near the leaf edge $\xi = \ell$.

Case (ii) If all pores are closed, then $u \leq 0$ for all ξ and at steady state eqs.(16) and (17) become:

$$(24) \quad 0 = \frac{d^2 \hat{z}}{d\xi^2}$$

$$(25) \quad 0 = -\hat{u} + \beta \hat{z}$$

Solving (24) and (25) according to the boundary conditions (18) and (19) gives

$$(26) \quad \hat{z} \equiv z_0, \quad \hat{u} \equiv \beta z_0$$

Here the closed pore assumption of $u \leq 0$ for all ξ requires, from (26), that $z_0 \leq 0$. Note that although the pores are equally closed for any value of $z_0 \leq 0$, their internal water status varies with z_0 . Thus a leaf with slightly negative z_0 requires a smaller change in water potential to open its stomata than a leaf which has a more negative z_0 , i.e., which is drier (even though both leaves have all stomata closed.)

A comparison of these two cases shows that the sign of the petiole potential z_0 determines which case occurs.

STABILITY OF THE STEADY STATE

In order to investigate the stability of the steady state solutions just obtained, we set

$$(27) \quad z(\xi, \tau) = \hat{z}(\xi) + Z(\xi, \tau),$$

$$(28) \quad u(\xi, \tau) = \hat{u}(\xi) + U(\xi, \tau),$$

where $\hat{z}(\xi)$ and $\hat{u}(\xi)$ are the steady states (23) or (26), and where $Z(\xi, \tau)$ and $U(\xi, \tau)$ represent small perturbations from steady state. The steady states will be said to be stable if all solutions Z and U remain bounded for all $\tau \geq 0$, and unstable if an unbounded solution exists.

Substituting (27) and (28) into (16)-(19) gives in the case in which all pores are open

$$(29) \quad \frac{\partial Z}{\partial \tau} = \frac{\partial^2 Z}{\partial \xi^2} - \alpha U$$

$$(30) \quad \frac{\partial U}{\partial \tau} = -U + \beta Z$$

$$(31) \quad Z = 0, \quad \xi = 0,$$

$$(32) \quad \frac{\partial Z}{\partial \xi} = 0, \quad \xi = \ell.$$

In the case in which all pores are closed, the equations governing stability can be obtained from (29)-(32) by taking $\alpha = 0$ (since this effectively removes the open pore sink term in eq.(29).)

We look for solutions to (29),(30) in the form

$$(33) \quad Z(\xi, \tau) = e^{r\tau} f(\xi)$$

$$(34) \quad U(\xi, \tau) = e^{r\tau} g(\xi)$$

which gives

$$(35) \quad r f = \frac{d^2 f}{d\xi^2} - \alpha g$$

$$(36) \quad r g = -g + \beta f$$

that is,

$$(37) \quad \frac{d^2 f}{d\xi^2} - \left[r + \frac{\alpha \beta}{1+r} \right] f = 0$$

Solving (37) and substituting (33) into the boundary conditions (31),(32) gives

$$(38) \quad f(\xi) = \sin \frac{n\pi}{2\ell} \xi, \quad n = 1, 3, 5, \dots$$

where

$$(39) \quad r + \frac{\alpha \beta}{1+r} = - \left[\frac{n\pi}{2\ell} \right]^2$$

Eq.(39) can be written as a quadratic on the characteristic exponent r :

$$(40) \quad r^2 + \left[1 + \left[\frac{n\pi}{2\ell} \right]^2 \right] r + \left[\alpha \beta + \left[\frac{n\pi}{2\ell} \right]^2 \right] = 0$$

Since all coefficients in eq.(40) are positive, the roots r are, by Descartes' Rule of Signs, either both negative, or are a complex conjugate pair. In the latter case, the quadratic formula shows that the real part is negative. Thus all steady state equilibria are stable.

Eq.(40) shows that there can exist a significant difference between the approach to open pore equilibrium and to closed pore equilibrium. In the case of all pores closed, we may take $\alpha = 0$ in (40), giving

$$(41) \quad r = -1 - \left[\frac{n\pi}{2\ell} \right]^2$$

which means that no oscillations are predicted to occur during the transient approach to closed pore steady state. In the case of open pore steady state, however, complex conjugate roots r may occur for certain values of n . Thus from (33),(34), the model predicts that the approach to open pore equilibrium may be accompanied by transient waves of stomatal opening.

NUMERICAL SIMULATION

In order to verify the foregoing results, we turn to numerical simulation of the model. An approximate solution to eqs.(16)-(19) was obtained using finite differences with 40 pivotal points in the ξ direction. Results are presented for these parameter values:

$$(42) \quad \alpha = 20, \quad \beta = 3/4, \quad \ell = 2.$$

Two cases are considered: (i) the leaf is initially in closed pore equilibrium (26) with $z_0 = -1$, when suddenly z_0 jumps to $+1$, and (ii) the leaf is initially in open pore equilibrium (23) with $z_0 = +1$, when suddenly z_0 jumps to -1 . Fig.3 shows the state of the pores (open or closed) as a function of ξ and τ . In case (i), the approach to open pore equilibrium is accompanied by two closed pore "echoes" which originate at the leaf edge $\xi = \ell$ and move into the leaf in a wave-like fashion. This behavior is in contrast to case (ii), in which the approach to closed pore equilibrium exhibits no such echoes.

The reason for the echoes is the predicted oscillations associated with complex roots r in eq.(40). This may be verified by examining the time history of z and u at the leaf edge $\xi = \ell$ in case (i), see Fig.4. Note the damped oscillations and the phase lag of $u(\ell, \tau)$ behind $z(\ell, \tau)$. The phase difference may be explained in words as follows: At a given station, the water potential z increases until the pore opens (when $u = 0$) and the leaf begins to lose water locally by evaporation, at which time z begins to decrease. Thus z achieves its maximum approximately when u goes through zero, cf. Fig.4. The ensuing drop in water potential eventually causes the pore to close, after which z increases, and so on. At stations far from the petiole (e.g. at $\xi = \ell$, Fig.4), z begins to decrease even before the local pores open. This is due to diffusion, since the pores at the petiole end $\xi = 0$ have already opened, and water shortages are already taking effect at $\xi = \ell$.

Note the absence of such oscillations in the comparable functions $u(\ell, \tau)$ and $z(\ell, \tau)$ for case (ii), see Fig.5.

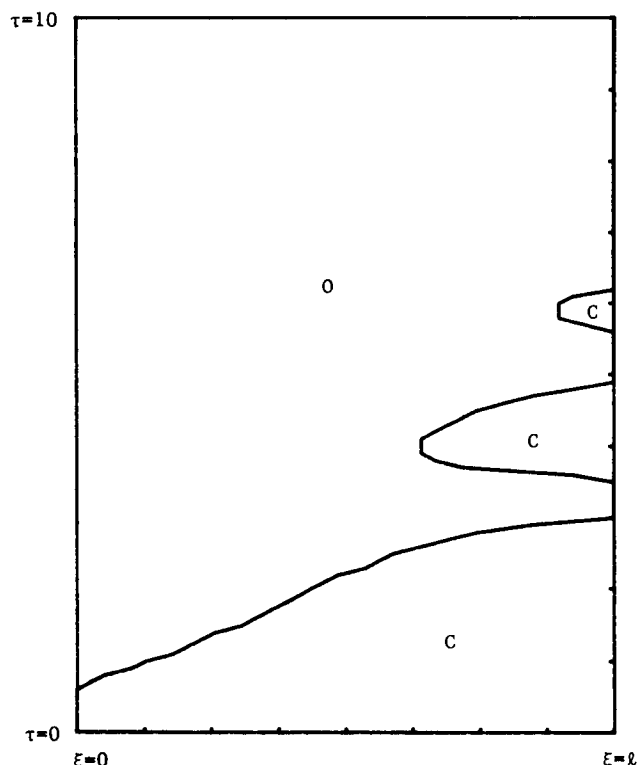


Fig.3(i). Pore state as a function of ξ and τ for case (i). O = Open, C = Closed.

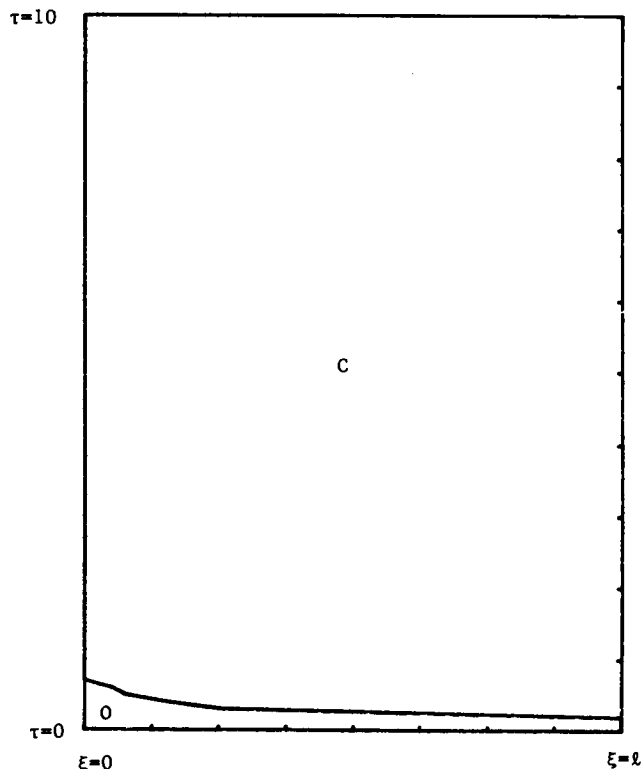


Fig.3(ii). Pore state as a function of ξ and τ for case (ii). O = Open, C = Closed.

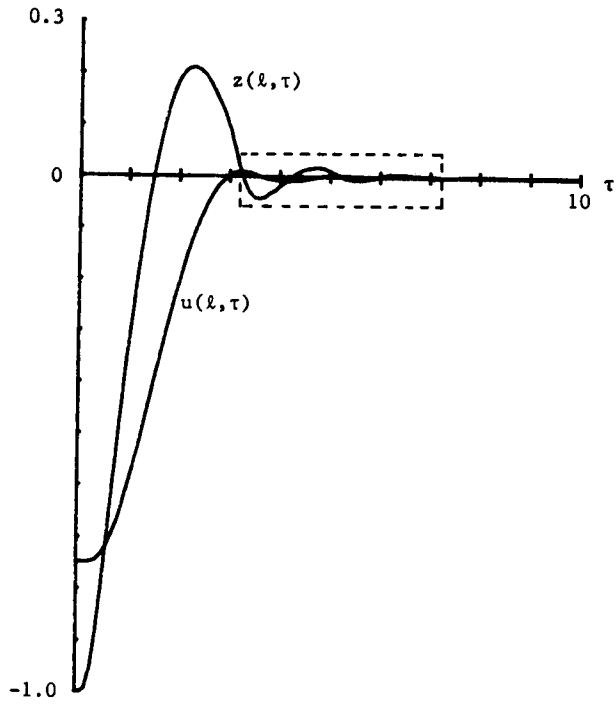


Fig.4a. $u(\ell, \tau)$ and $z(\ell, \tau)$ for case (i). See Fig.4b for blowup of region enclosed by dashed lines.

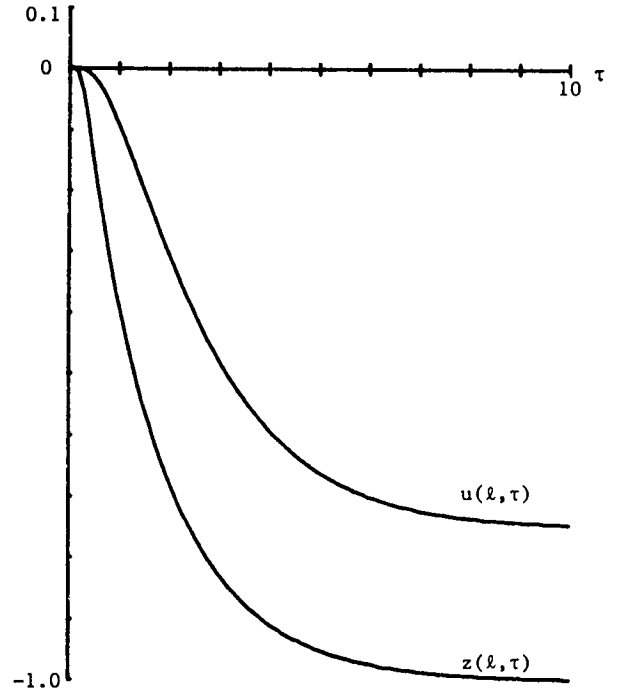


Fig.5. $u(\ell, \tau)$ and $z(\ell, \tau)$ for case (ii).

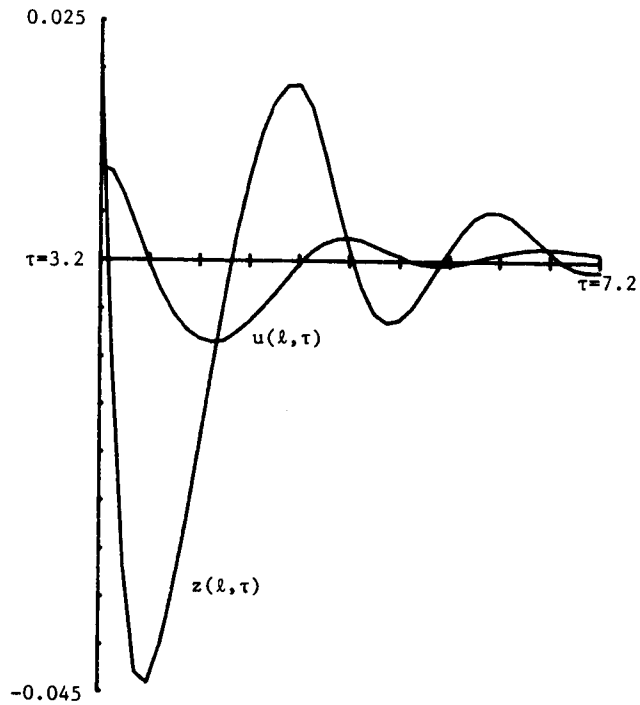


Fig.4b. $u(\ell, \tau)$ and $z(\ell, \tau)$ for case (i). Blowup of region enclosed by dashed lines in Fig.4a.

SUMMARY AND CONCLUSIONS

This work presents the derivation and analysis of a model of the dynamics of stomates in leaves. For appropriate parameter values the model exhibits a series of small amplitude transient waves of stomatal opening in response to the sudden availability of water. In the opposite case in which the supply of water becomes suddenly inadequate, the model exhibits no such oscillations, but rather predicts the gradual spread of the transition from open to closed stomates.

Note that the oscillations during opening are due to the interaction between the local stomate model, eq.(17), and the diffusion equation governing leaf water potential, eq.(16). E.g., if eq.(16) was replaced by the assumption that the water potential z was constant in time throughout the leaf, then eq.(17) would exhibit a damped non-oscillatory guard cell pressure-pore width u .

The additional ingredient which models of stomate fields in the whole leaf ([20],[2], and this work) add to models of an individual stomate ([14]-[17]) is a mechanism by which a given stomate can influence and be influenced by the behavior of neighboring stomates. Both in this work and in [2], this mechanism (the diffusion of water potential) enhances the oscillatory dynamics for appropriate model parameters. The result is spatial dependence of the oscillation, i.e. waves.

This kind of model is mathematically similar to reaction-diffusion equations which have found application in numerous other biomathematics problems. Pattern formation and waves have been observed using similar models in the areas of morphogenesis, neurobiology, slime mold aggregation, etc. [22]. In comparison with these related models, the present application to stomatal dynamics involves a characteristic nonlinearity due to the essential appearance of the Heaviside step function (eqs.(2),(16)) corresponding to the impossibility of negative pore widths.

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