

HANDBOOK OF FLUID DYNAMICS AND FLUID MACHINERY

VOLUME III: APPLICATIONS OF FLUID DYNAMICS

Edited by

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24.6 FLUID MECHANICS IN PLANT BIOLOGY

Richard H. Rand and J. Robert Cooke

24.6.1 Introduction

In this section, we describe a variety of phenomena associated with fluid flow in green plants and summarize some attempts to model these effects. We begin by giving a schematic engineering description of the biofluid mechanics of a green plant. The leaves, vascular structure, and roots of a green plant may be thought of as functioning to support the conversion of energy from sunlight into the chemical energy stored in sugars via the process of *photosynthesis*. The chemistry of photosynthesis requires sunlight, CO_2 and water and produces glucose (a simple sugar) and O_2 . This process takes place in the leaves, and the manufactured sugars are *translocated* to other parts of the plant via the vascular *phloem* tissue. The water required for photosynthesis is absorbed through the roots, and the necessary CO_2 is

found in the ambient atmosphere and enters the leaf by diffusion. Note the contrast with gas exchange in humans, where muscles power breathing, producing a mass flow of fresh air into our lungs. Diffusion is driven by a concentration difference and is effective only over short distances, which is why leaves are relatively thin structures. Accompanying the entry of CO_2 into the leaf is the loss of water vapor by evaporation and diffusion. This loss tends to desiccate the plant, and water lost by evaporation in the leaves is replenished via the vascular *xylem* tissue, resulting in an upward flow called the *transpiration stream*. In contrast to the human circulatory system, which is closed, the vascular system of plants is open. It involves extensive branching at both the leaves and roots. The roots function to absorb the necessary water from the soil, as well as to absorb minerals, store carbohydrates, and anchor the plant in the soil.

A variety of sources are available for an introduction and overview of the engineering aspects of green plants. Nobel (1974, 1991) contains an extensive quantitative introduction and order of magnitude analysis. Merva (1975) presents a shorter quantitative introduction. Meidner and Sheriff (1976) and Milburn (1979) offer introductions which use engineering concepts with a minimum of mathematics. Canny's (1977) brief nonmathematical introduction is aimed at fluid mechanics. The present authors have attempted several brief summaries. Cooke and Rand (1980) reviewed leaf diffusion models, Cooke (1983) summarized stomatal dynamics and gas exchange, and Rand (1983) presented an overview of fluid dynamics in green plants. Niklas (1992) provides a review of plant biomechanics in relation to plant form and function. The general context for fluid motion in plants is covered in the introductions to plant physiology by Galston *et al.* (1980), Taiz (1991), and Salisbury and Ross (1992). Greater detail is provided in the specialized surveys by Crafts and Crisp (1971), Esau (1977), Jarvis and Mansfield (1981), Zimmerman (1983), Zeiger *et al.* (1987), and Fahn (1990).

24.6.2 Basic Concepts

Water moves in plants as a result of gradients in chemical concentration (cf. *Fick's law*), hydrostatic pressure, and gravitational potential. Plant physiologists have found it convenient to deal with these diverse effects by using a single quantity, a chemical potential called the *water potential*, ψ [Nobel (1974), (1991)]

$$\psi = p - RTc + \rho gz \quad (24.155)$$

where p is hydrostatic pressure (bar), R is the gas constant = $83.141 \text{ cm}^3\text{-bar/mol K}$, T is temperature (K), c is concentration of all solutes in an assumed dilute solution (mole/cm^3), ρ is the density of water (g/cm^3), g is the acceleration of gravity = 980 cm/sec^2 , and z is height (cm). Here, ψ is in bars, a convenient unit commonly used in plant studies for measuring pressure. (One bar equals 10^6 dyne/cm^2 and is approximately equal to one atmosphere.)

An individual plant cell consists of a cell wall surrounding a cell membrane (the *plasmalemma*), inside of which lies the cell protoplasm (see Fig. 24.42). In order for the cell to be in equilibrium with its surrounding medium, the water potential inside the cell must equal the water potential outside the cell. However, since the plasmalemma is able to maintain a concentration difference between the interior and

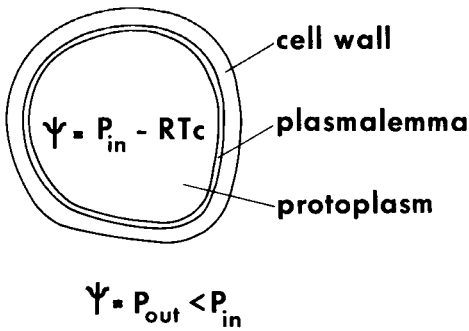


FIGURE 24.42 Schematic diagram of a typical plant cell. For equilibrium, the water potential, ψ , inside the cell must equal that outside the cell.

the exterior of the cell, the hydrostatic pressure inside the cell can be larger than that outside the cell from Eq. (24.155). This situation (of which there is no parallel in the case of animal cells) is resolved by the elastic extension of the plant cell wall, creating a *turgor* (hydrostatic) pressure inside the cell.

An important concept for understanding the flow of water in plants is the distinction between the *symplasm* and the *apoplasm*. The symplasm consists of all the protoplasm (inside the plasmalemma) of all the living cells of the plant, together with the plasmodesmata (thin strands of cytoplasm that go from the interior of a given cell, through the cell wall, and into the interior of a neighboring cell). In terms of *point set topology*, the symplasm is thought to be a *connected set*. The apoplasm consists of those regions of the plant that contain water and are not in the symplasm. In particular, the apoplasm includes the xylem (which consists of dead cells), as well as the fluid in the cell walls of all the cells of the plant. Flow in the symplasm has been estimated to involve a resistance about 50 times as large as that in the apoplasm [Meidner and Sheriff (1976)], although more recent work contests this view [Canny (1993)].

24.6.3 Stomata

A typical leaf of a green plant shown in Fig. 24.43 is filled with *mesophyll cells* which contain the chlorophyll necessary for photosynthesis. These cells are sandwiched between the outer layers of the leaf which consist of epidermal cells covered with a layer of waxy material called *cutin*, which inhibits the loss of water through the surface of the leaf. CO_2 enters the leaf through small holes in the epidermis called *stomata* (or stomates) [Meidner and Mansfield (1968)]. An individual stomate is composed of two specialized cells called *guard cells*. Figure 24.43(c) illustrates the kidney-shaped stomata. A bar-bell shape is common in grasses. Like all cells in a green plant, the guard cell has a cell wall in addition to the cell membrane present in animal cells. This gives the plant cell elastic stiffness, an effect which is enhanced if the cell is *turgid*, i.e., if the cell membrane (or plasmalemma) exerts a hydrostatic pressure on the cell wall due to a solute concentration difference between the interior and the exterior of the cell. In the case of a guard cell, the change in shape upon hydrostatic loading results in a change in the size of the stomatal pore.

When the stomatal pore is open, water vapor diffuses out of the leaf, because the water concentration within the plant is normally higher than in the ambient air. When CO_2 is not needed for photosynthesis, e.g., at night, the stomata can close, acting

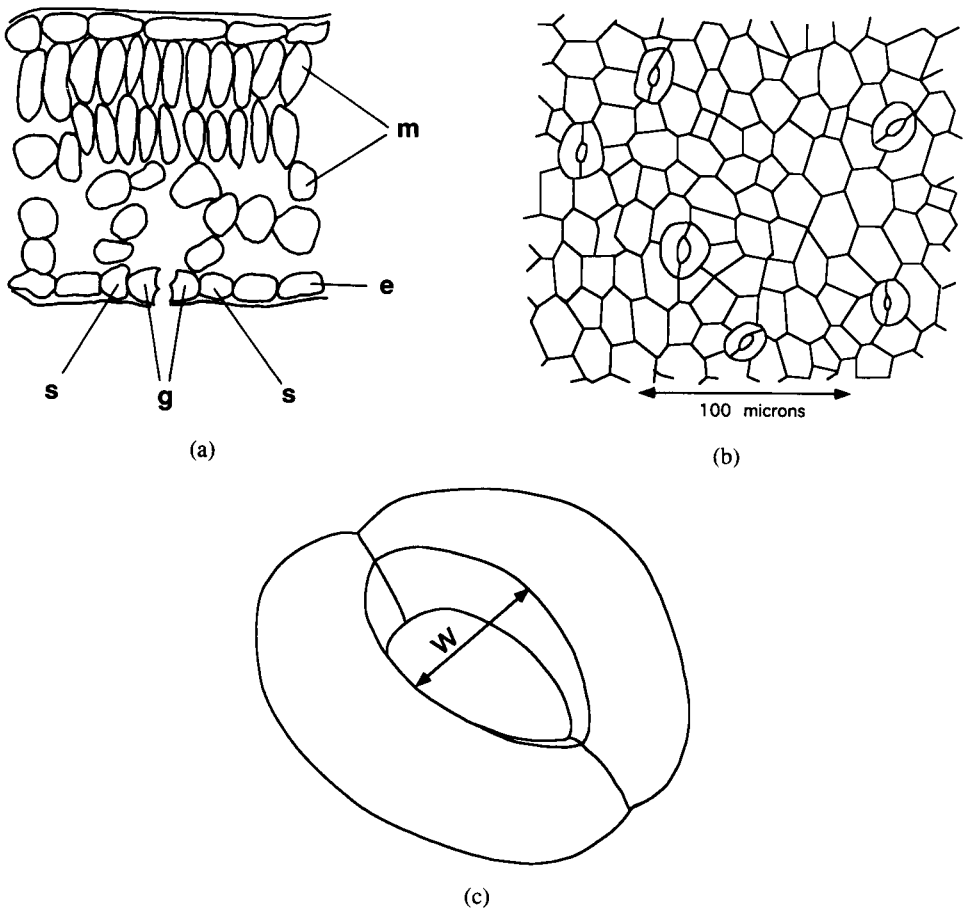


FIGURE 24.43 Typical leaf of a green plant. (a) Schematic diagram of a transverse section of a leaf (after Nobel, 1974). A representative value for leaf thickness is $300\ \mu\text{m}$. *m* = mesophyll cell, *e* = epidermal cell, *g* = guard cell, and *s* = subsidiary cell. (b) Stomatal pores on the leaf surface and (c) a pair of guard cells surrounding a stomatal pore; *w* = pore width.

like valves in a feedback control system to limit water loss. They similarly close when the plant is experiencing *water stress*, i.e., extreme dryness due to lack of rain. For this reason, a great deal of attention has been given to studies of related phenomena, such as diffusive flow through the stomatal pores, the elastostatics of guard cells, and the dynamical behavior of stomata.

How do stomata open and close? Many older plant physiology texts explain this by stating that the walls of the guard cells next to the pore are thicker than the walls on the side away from the pore. They imagine that upon inflation, the outer wall buckles outward, pulling the rest of the guard cell with it and opening the pore. Here is a situation where an engineering approach can clarify things. Cooke *et al.* (1976) have modeled the guard cell as a linear anisotropic thin shell. Using finite element analysis they showed that an increase in hydrostatic pressure in the guard cell (for fixed pressure in neighboring subsidiary cells) tended to open the pore. On the other

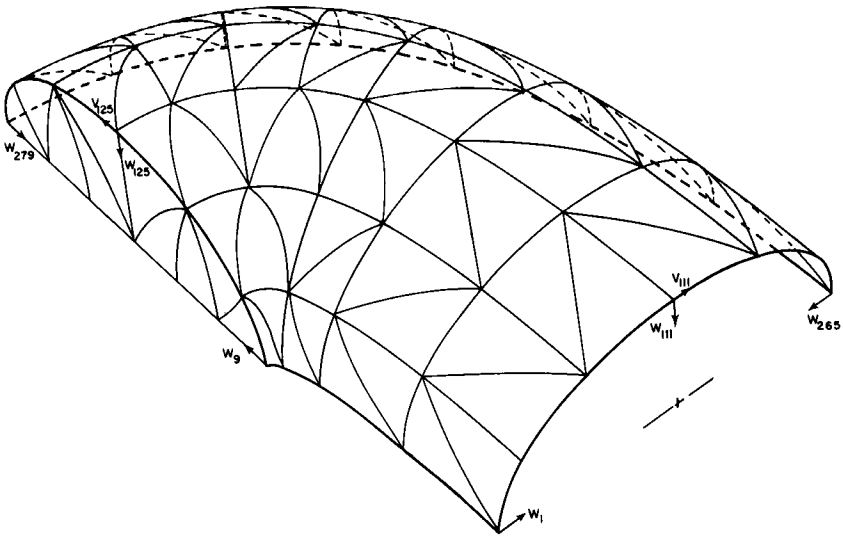


FIGURE 24.44 A finite element discretization of a quadrant of a guard cell. (Reprinted with permission, Cooke, J. R., Debaerdemaker, J. G., Raud, R. H., and Many, H. A., "A Finite Element Shell Analysis of Guard Cells Deformations," *Trans. ASAE*, Vol. 19, pp. 1107-1121, 1976.)

hand, an increase in pressure in neighboring subsidiary cells (for fixed pressure in the guard cell) tended to close the pore (see Fig. 24.44). It was shown that the elliptical shape of the guard cell is critical for opening, and that other features such as wall thickening and radial stiffing (due to the micellae, i.e., radial cellulose microfibrils) could help the opening process, but were not essential for static opening. The effect of the radial stiffing is to permit a smaller pressure fluctuation in the subsidiary cell to counteract a larger pressure fluctuation in the guard cells during the pore opening and closing cycle. The work on the structural analysis was extended by Cooke *et al.* (1977) to include nonlinear effects. When the geometric nonlinearities are included, the pore width, as expected, is shown to plateau as pressure within the guard cell increases.

A problem related to the gaseous fluxes in the leaf concerns the dynamic behavior of the stomatal apparatus. Experimental observations have revealed that the width of the stomatal pore often oscillates, typically with a period ranging from 10 to 50 min. Delwiche and Cooke (1977) modeled this phenomenon by balancing water fluxes between the guard cell, the subsidiary cell, and the rest of the plant. The gaseous flux through the stomatal pore can oscillate periodically under stress conditions—even when all ambient conditions remain constant. The stomatal apparatus acts as a feedback control system. The oscillatory gaseous flux may be described as follows. Water evaporating from the wet mesophyll and subsidiary cell walls diffuses through the stomatal pore to the leaf exterior. This water is replaced both by a flux from the roots via the xylem and by a flux from the guard cells to the subsidiary cells. The resulting decrease in hydrostatic pressure in the guard cells causes the stomatal pore width to decrease [Delwiche and Cooke (1977)]. A smaller pore width slows the rate of evaporation, increasing the water potential in the mesophyll

and causing water to accumulate there. In response to this accumulation, water diffuses back to the guard cells, increasing their hydrostatic pressure and increasing the pore width. The model takes the form of an *autonomous* system of two first-order ordinary differential equations for p_g and p_s (the pressures in the guard and subsidiary cells). The resulting flow in the $p_g - p_s$ plane exhibits a *limit cycle* as illustrated in Fig. 24.45. Note that a limit cycle is a strictly nonlinear phenomenon and is due here to the piece-wise linear nature of the relation between pore width w and p_g, p_s . The piece-wise linearity follows from the fact that w can never become negative (even with a linear elastic model of the guard cell).

This work was extended by Rand *et al.* (1981) by embedding the original system of Delwiche and Cooke (1977) into a one-parameter family of systems. It was found that as the parameter (which represents the concentration of the osmotically active solutes in the guard cell) is varied, the dynamical properties exhibited by the system change (see Fig. 24.46). The system was shown to contain a *Hopf bifurcation* [Rand *et al.* (1981) and Rand (1994)] that involved the genesis of an unstable limit cycle. The oscillatory behavior was seen as a kind of dynamical bridge between the open and closed pore equilibrium states. Upadhyaya *et al.* (1980a,b) extended the Delwiche and Cooke (1977) model by including CO_2 feedback effects. This involved modeling the guard cell biochemistry in order to include a CO_2 sensor in the system. The model displayed a limit cycle oscillation, which involved a 2 min CO_2 -based oscillation superimposed on the 20 min. water-based oscillation previously discussed (and shown in Fig. 24.45), in agreement with the experimental observations of other investigators.

Oscillatory plant transpiration has been observed in numerous plants and explored experimentally. Gumowski (1981) suggested that the oscillatory behavior avoids prolonged high rates of stomatal transpiration and reduces the internal energy expenditure required for the maintenance of turgor. Upadhyaya *et al.* (1981), (1988),

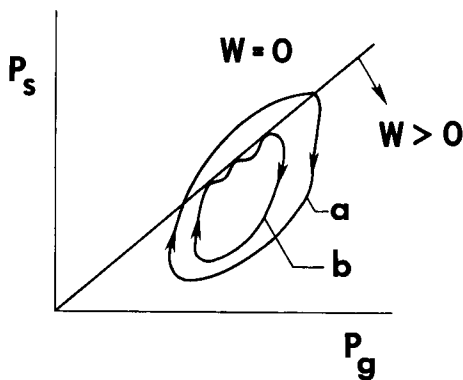


FIGURE 24.45 Limit cycles representing stomatal oscillations in the $p_g - p_s$ plane. Here p_g and p_s represent hydrostatic pressures in guard and subsidiary cells respectively, and w represents pore width. The region above the straight line corresponds to a closed pore ($w = 0$). The arrow perpendicular to the straight line shows direction of increasing pore width. Path a—stomatal oscillation due to hydraulic feedback loop only. (From Delwiche and Cooke, 1977.) Path b—stomatal oscillation due to both hydraulic and CO_2 feedback effects. (From Upadhyaya *et al.*, 1980a,b.)

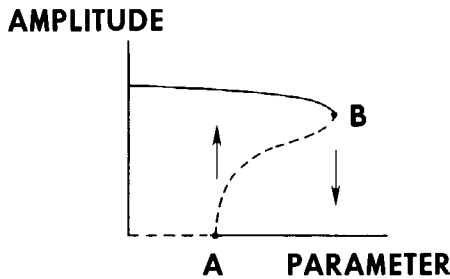


FIGURE 24.46 Changes in the amplitude of the stomatal oscillation of Fig. 24.45 due to changes in a system parameter. (From Rand *et al.*, 1981.) Zero amplitude corresponds to equilibrium behavior. The dashed and solid lines correspond to unstable and stable motions respectively. At point *A* an unstable equilibrium point becomes stable and throws off an unstable limit cycle (a Hopf bifurcation.). At point *B* a stable and an unstable limit cycle coalesce. Arrows represent jump phenomena.

when considering the carbon dioxide feedback loop, independently and simultaneously proposed that the oscillatory behavior reduces water losses while preserving carbon dioxide uptake at minimal levels.

Why do stomata oscillate? That is, in terms of Darwinian evolution, of what advantage to the plant are stomatal oscillations? Upadhyaya *et al.* (1981) investigated this question by comparing gaseous fluxes through a stomatal pore in an open equilibrium state with fluxes through an oscillating pore. For typical values of the system parameters, they found that stomatal oscillations tend to conserve water under relatively dry, i.e., water stressed atmospheric conditions. However, this savings in moisture content occurs at the expense of a reduction in the CO_2 assimilation rate.

Experimental work [Ellenson and Amundson (1982) and Mott *et al.* (1993)] has shown that the process of opening and closing of stomata varies across the leaf surface and involves complicated dynamics taking the form of *waves* of stomatal opening. This organized behavior implies fluid dynamical coupling between the individual stomata. This has been modeled [Rand *et al.* (1982), Rand and Ellenson (1986), and Rand (1987)] by permitting the water potential, ψ , in the leaf to be a field quantity, i.e., $\psi = \psi(x, y, t)$ where x and y measure the position of a point on the leaf surface. ψ satisfies a diffusion equation with a distributed sink term, $Q(w)$, corresponding to the loss of water vapor due to evaporation through open stomatal pores

$$\frac{\partial \psi}{\partial t} = D \left[\frac{\partial^2 \psi}{\partial x^2} + \frac{\partial^2 \psi}{\partial y^2} \right] - Q(w) \quad (24.156)$$

where again w is the local pore width. The function $Q(w)$ is essentially nonlinear, since water loss Q is a monotone increasing function of w for $w > 0$, while $Q = 0$ for $w < 0$. The partial differential equation on ψ is accompanied by boundary conditions such as no flux at the leaf edge, or given ψ at the leaf midrib. The dynamics of an individual stomate have been modeled in a variety of ways [Rand *et al.* (1982), Rand and Ellenson (1986), and Rand (1987)], but all involve coupling to other sto-

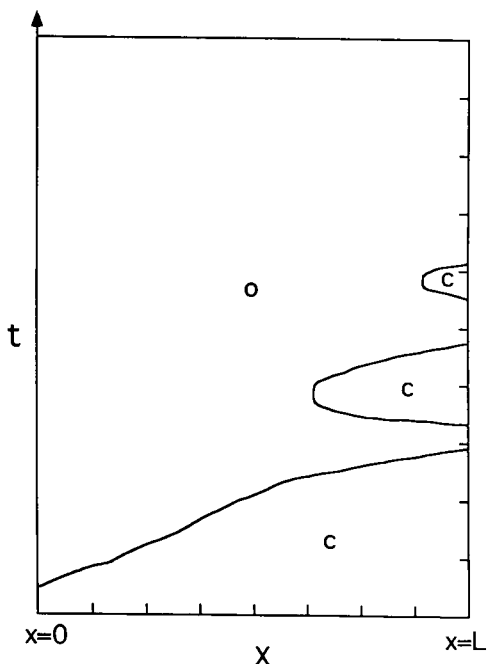


FIGURE 24.47 Pore state displayed as O = open or C = closed in the x - t plane. Here $x = 0$ corresponds to the midrib and $x = L$ to the leaf edge. (From Rand, 1987.)

mata, e.g., by dependence on local water potential, ψ . As an example of the prediction of such a model, imagine a leaf which has all its stomata closed, e.g., due to a condition of water stress at the roots, when suddenly the availability of water is increased. This corresponds in the model to a jump in the boundary value of ψ and may result in the eventual opening of all the stomata on the leaf surface. However, the dynamical behavior is wave-like, and may involve *echoes*, as shown in Fig. 24.47 [Rand and Ellenson (1986) and Rand (1987)].

Before leaving this topic, we note that Cooke *et al.* (1988) have provided a computer-based introduction to stomatal dynamics.

24.6.4 The Transpiration Stream

Water which enters the plant through the roots rises through the xylem vascular tissue to the leaves, where it evaporates. A natural question concerns how it is possible for the transpiration stream to reach the tree top. Since the pressure exerted by the atmosphere corresponds to a gravitational head of only about ten meters, this process cannot be explained by the creation of a vacuum somewhere in the plant. In fact, the explanation lies in the leaves, where the site of evaporation is the menisci in the mesophyll cell walls. These liquid-air interfaces are bounded by the strands of cellulose that constitute the cell wall. A representative interfibrillar space has a diameter of about $0.01 \mu\text{m}$ [Nobel (1974)]. The pressure difference across a spherical meniscus is given by

$$\Delta p = 2\sigma/r \quad (24.157)$$

where σ is the surface tension coefficient = 73 dyne/cm for an air-water interface at 20°C and r is the radius of curvature of the meniscus (cm). Here, Δp is about

300 bars or about 3000 meters of gravitational head, thus easily accounting for the ascent of water to the tops of the highest trees. Of course, this requires that the continuous fluid column reaching from the roots to the leaves be under considerable tension. Although the theoretical tensile strength of a perfect column of water greatly exceeds 300 bars [Hammel and Scholander (1976) and Nobel (1974)], the presence of small air bubbles and other imperfections reduces the observed tensile strength in laboratory experiments. Nevertheless, the plant is evidently able to maintain a vascular system relatively free from air bubble defects. The phenomenon of xylem cavitation has been studied extensively by Tyree (1991).

The dynamics of a spherical evaporating meniscus has been studied by Rand (1978a). The analysis involved a nonlinear differential-integral equation and predicted damped oscillatory motions for a certain range of parameter values.

The flow of water along the transpiration stream in the leaf proceeds through the branching xylem system to the xylem termini, and it then continues through the apoplastic mesophyll cell walls and symplast to those mesophyll cells near the stomatal pore where evaporation occurs. Stroshine *et al.* (1979, 1985) have studied flow in the leaf and stem. This involves consideration of branching xylem vessels of various sizes as well as a diffusive flow between the xylem and the leaf symplasm (the interior of the mesophyll cells). It was concluded that the large vascular bundles offer relatively little resistance to flow compared with the intermediate and small bundles. This shows the advantage of a branching structure to the vascular system.

24.6.5 Gaseous Diffusion

The problem of gas exchange in leaves was first investigated from a mathematical point of view in a classic paper by Brown and Escombe (1900). By modeling the leaf surface as a plane septum with a circular hole and the pore as a circular cylinder, they explained the experimentally observed relatively large rates of transpiration from leaves (comparable to evaporative fluxes from an equal-sized body of water). Bange (1953) used an approximate analysis in order to consider a realistic geometry for the leaf interior as well as a still air layer outside the leaf. He found that as the wind speed increased, i.e., as the thickness of the still air boundary layer decreased, the stomata played an increasingly important role in controlling gaseous fluxes. Although a wider pore always results in a larger flux, this effect was shown to be negligible for relatively thick boundary layers. Cooke (1967) considered diffusion through an elliptical pore. Using a relationship involving complete elliptic integrals, he showed that a slightly open stomate can permit relatively large diffusion rates. For example, an ellipse with a major to minor axis ratio of 20 has a discharge rate that is 39% of that of a circle of diameter equal to the major axis. Cooke (1969) and Holcomb and Cooke (1977) considered the interaction effects between neighboring stomatal pores. Using separation of variables, they showed that the flux depends on both the spacing between stomata on the leaf surface and the boundary-layer thickness; Fig. 24.48. In particular, the overall diffusion rate from a leaf was shown to not depend linearly on the area of the pores.

Is there an optimal spacing for stomata that will maximize gaseous exchange? Holcomb and Cooke (1977) sought to answer this question by using the analogy between diffusion and the flow of electric current in an aqueous electrolyte solution. They built an electrolytic tank (copper sulphate in a copper and plexiglass container) and used it to study the effects of pore eccentricity, stomatal spacing, boundary-

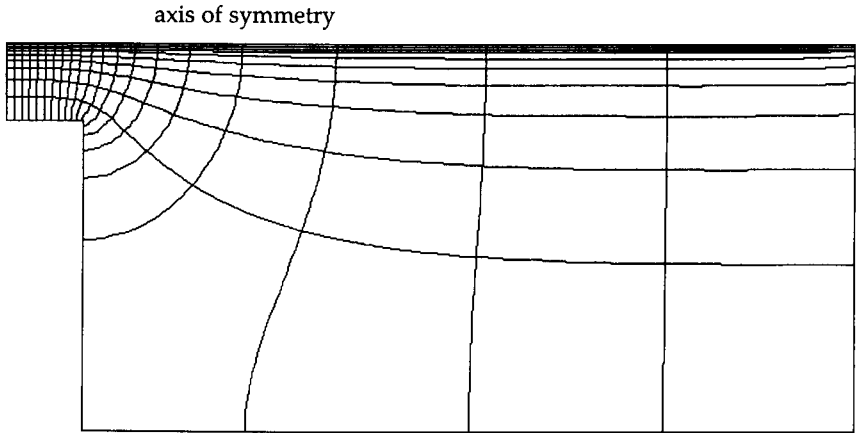


FIGURE 24.48(a) Diffusion from neighboring stomatal pores. Surfaces of constant partial pressure and lines of diffusion for a stomatal pore modeled as a circular cylinder (at bottom of figure). The atmosphere adjacent to the leaf is also modeled as a circular cylinder (located above the stomatal pore). Concentrations are fixed at the bottom and top surfaces of the figure, and zero flux is assumed at the radial boundaries and at the leaf surface.

layer thickness, and pore depth (see Fig. 24.49). The diffusion rate (per unit leaf area, not per pore) increases monotonically with increasing pore width, with decreasing pore spacing and with decreasing boundary layer thickness. Thus, there is no optimal pore spacing to maximize diffusion rate *per unit leaf area*. In a mathematical sense, as the pore area increases, the passive diffusion rate can approach, but not exceed, that of a free body of water. Note that a relatively thick boundary layer causes the stomate to function as an on-off valve. Parlange and Waggoner (1970) used conformal mapping to study diffusion through a two-dimensional slit. They compared their results with the formula of Brown and Escombe (1900) and found the approximation inherent in the latter to be best for thin, deep slits.

Most studies of gaseous diffusion in leaves have assumed the *cuticle* (i.e., the cutinized epidermal surface) to be completely impermeable. Although diffusion oc-

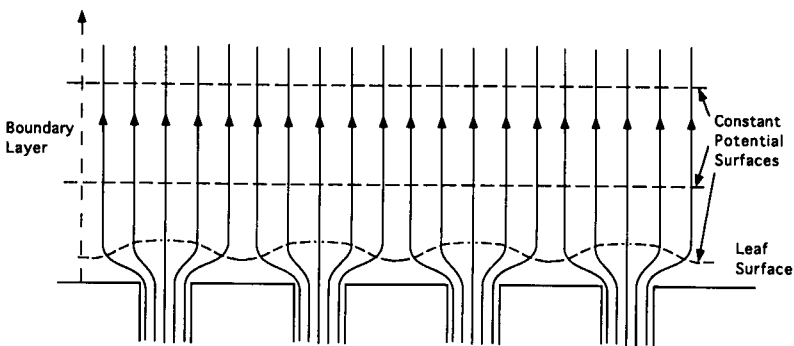


FIGURE 24.48(b) Sketch of diffusion streamlines away from an array of stomates. (Reprinted with permission, Holcomb, D. P. and Cooke, J. R., "An Electrolytic Tank Analog Determination of Stomatal Diffusion Resistance," ASAE Paper No. 77-5510, 1977.)

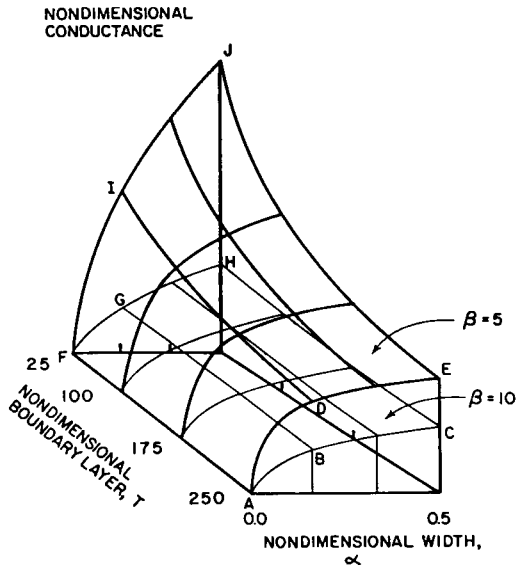


FIGURE 24.49 A nondimensionalized display of stomatal diffusion rate as a function of nondimensional pore width (α), boundary-layer thickness (T), and stomatal spacing, (β). [Reprinted with permission, Cooke, J. R. and Rand, R. H., "Diffusion Resistance Models," *Predicting Photosynthesis for Ecosystem Models*, Hesketh, J. D. and Jones, J. W. (Eds.), Vol. 1, pp. 93–121, CRC Press, 1980.]

curs primarily through the stomata, there are some species, such as ferns (which have a very thin cuticle), in which 30% of the total diffusion rate can occur through the cuticle. Hsu and Ganatos (1983) have modeled this situation as a boundary value problem. They found that cuticular diffusion was decreased as the stomata were spaced closer together.

Current treatments of gaseous diffusion in the leaf [see, for example, Nobel (1991)] utilize a one-dimensional model which, by analogy with Ohm's law, involves a series of resistances, each associated with a portion of the pathway. This is depicted in Fig. 24.50. Parkhurst (1977) compared a three-dimensional field equation approach with the commonly used one-dimensional resistance model and found that the latter involved an error of 44%. Nearly all studies of leaf diffusion have assumed steady-state diffusion. Gross (1981), however, included time-dependent terms in order to estimate the time scale of the gaseous diffusion process. He found equilibrium to be essentially attained in less than one second.

Webster (1981) has applied the concept of the *effectiveness factor* to leaf diffusion in order to gauge the extent to which assimilation is diffusion limited. This factor is defined as the ratio of the actual assimilation rate to the assimilation rate that would occur in the absence of any CO_2 concentration gradients. An effectiveness factor of unity indicates that assimilation is kinetically limited, while a value considerably smaller than unity indicates that losses due to diffusion are significant.

Open stomatal pores allow CO_2 to diffuse into the leaf interior where it is converted into sugars by photosynthesis. At the same time, water vapor may evaporate from the wet mesophyll cell walls and diffuse out of the leaf interior into the neigh-

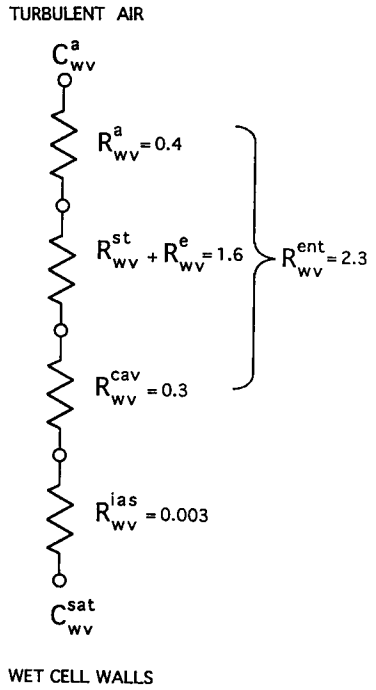


FIGURE 24.50 Electrical circuit analogy for steady state diffusion of water vapor in a leaf. [Reprinted with permission, Cooke, J. R. and Rand, R. H., "Diffusion Resistance Models," *Predicting Photosynthesis for Ecosystem Models*, Hesketh, J. D. and Jones, J. W. (Eds.), Vol. 1, pp. 93-121, CRC Press, 1980.] C_{wv}^a = concentration of water vapor in the turbulent atmosphere adjacent to the leaf. C_{wv}^{sat} = concentration of water vapor at the mesophyll cell evaporation sites. R_{wv} = resistance values in sec/cm. Superscripts: a = boundary layer adjacent to leaf, st = stomatal pore, e = end effect correction, cav = substomatal cavity, ent = entry region, and ias = intercellular air space.

boring atmosphere. Although these two diffusion processes appear to be entirely analogous, experimental work [Aston and Jones (1976), Tyree and Yianoulis (1980), and Canny (1993)] has shown that water vapor actually evaporates only from those cell walls which are near the stomatal pore, whereas CO_2 is absorbed into cells throughout the interior of the leaf, including those cell walls which are far from the stomatal pores. Although the diffusion coefficient of water vapor in air is about 1.6 times that of CO_2 in air, this difference (due to the different atomic weights of water vapor and CO_2) is insufficient to account for their difference in performance. Indeed, plant physiologists have been led to conjecture that the mesophyll cell walls far from the stomatal pores are covered with a special layer of cutinized material which inhibits the evaporation of water. No such assumption is needed, however, since the difference in behavior can be explained by the different roles that water vapor and CO_2 play in the physical chemistry of the leaf. Since the liquid in the cell walls of the leaf is a dilute aqueous solution in which water is the solvent and CO_2 the solute, the concentration of water vapor is governed by Raoult's Law, whereas that of CO_2 is governed by Henry's Law. This results in similar differential equations for the gas concentrations c of water vapor and CO_2 [Rand (1977a,b)]

$$\frac{\partial^2 c}{\partial x^2} - \alpha^2 c = 0 \tag{24.158}$$

where x measures distance along an intercellular pathway and α is a constant that is about 50 times larger for water vapor than for CO_2 . For suitable boundary conditions and typical leaf dimensions, this means that most water evaporation occurs within

the first 4% of the pathway near the substomatal cavity, whereas 87% of the pathway is needed for comparable CO_2 absorption.

After diffusing as a gas to the mesophyll cell walls, CO_2 continues to diffuse as a solute to the chloroplasts in the cell interior. Sinclair *et al.* (1977) and Sinclair and Rand (1979) have modeled this process by assuming spherical cell geometry and Michaelis–Menten reaction kinetics [Thornley (1976)]. The resulting nonlinear ordinary differential equation for CO_2 concentration as a function of radial position was solved approximately by perturbation methods. Expressions for the rate of CO_2 assimilation by a single cell were obtained in terms of cell size and biochemical parameters. This spherical cell model was incorporated into a more comprehensive model for CO_2 assimilation by Rand and Cooke (1980). The model took account of the gradual absorption of CO_2 into the mesophyll cell walls as CO_2 diffuses inward (i.e., diffusion with a distributed sink), as well as the effects of variation in cell-packing density. An approximate formula for CO_2 flux into the leaf in terms of basic geometrical and biochemical parameters was obtained by perturbations.

24.6.6 Flow in the Xylem and Phloem

The main conduits for fluid flow in the stem of plants consist of the xylem, through which the transpiration stream flows, and the phloem, through which sugars produced in the leaves are translocated to other parts of the plant. The conduits of plants are formed by individual plant cells placed adjacent to one another. During cell differentiation the common walls of two adjacent cells develop holes [called *pits* or *pores*; see Esau (1965)], which permit fluid to pass between them. The xylem contains *tracheids* and *vessel elements* (Fig. 24.51) that die after reaching maturity, while the phloem contains *sieve elements* that remain metabolically active. The Reynolds number for flow in the xylem is about 0.02 [Rand (1983)], which is best modeled by slow viscous (*creeping*) flow [Happel and Brenner (1965)], in which the inertia terms are neglected in the Navier–Stokes equations. The plant physiologist needs to know the pressure drops involved in flow through the vascular tissue. Such questions arise, for example, in the evaluation of various conjectured mechanisms for driving the phloem flow.

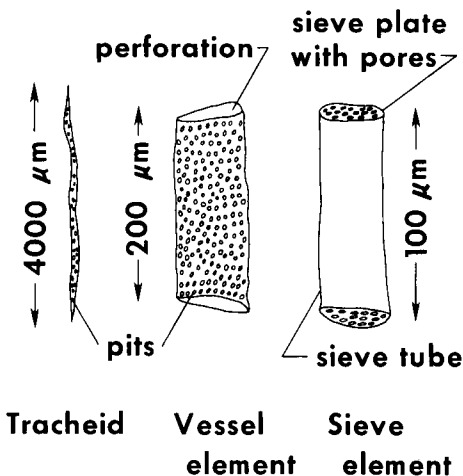


FIGURE 24.51 Fluid-conducting cells in the vascular tissue of plants (after Esau, 1965). Tracheids and vessel elements are found in the xylem, while sieve elements are found in the phloem. Here and in the rest of this paper, the dimensions given are typical but do not represent statistical averages.

The fluid mechanics of phloem flow has been considered by Rand and Cooke (1978) and Rand *et al.* (1980). As shown in Fig. 24.51, this involves flow through a series of cylindrical sieve tubes separated by perforated sieve plates. Due to the mathematical complexities of slow viscous flow, only the relatively unrealistic axisymmetric case of a single pore has been considered. The boundary value problem involved the field equations

$$\nabla p = \mu \nabla^2 \bar{v} \tag{24.159}$$

$$\nabla \cdot \bar{v} = 0 \tag{24.160}$$

with $\bar{v} = 0$ on the boundary, which was modeled as two circular cylinders in series, periodically repeated. The solution involved modified Bessel functions of the first kind, which turned out to be nonorthogonal. The results of the analysis were compared with Poiseuille's Law (which provides the standard approach currently used by plant physiologists). Poiseuille's Law, when applied to the sieve tube and the pore in series, was found to underestimate the exact pressure drop by about a factor of two.

Flow between two neighboring xylem tracheid cells occurs through pits (see Fig. 24.51). A typical bordered pit (in a conifer) consists of a circular border that arches over the pit cavity and contains a closing membrane (Fig. 24.52). The closing membrane is composed of a thick central region, which is relatively impermeable to the flow of fluid and a thin perforated peripheral region through which flow is possible. In nature, the bordered pit is found in both open and closed states. In the open state, flow is possible from one tracheid to another, while in the closed state virtually no flow occurs through the pit. This problem was studied by Chapman *et al.* (1977) by assuming an ideal fluid and using conformal mapping. The thin peripheral region of the closing membrane was modeled as linear springs, and equilibrium for a given flow rate was obtained by balancing the net hydrodynamic force on the central region of the closing membrane with the elastic restoring force of the peripheral region.

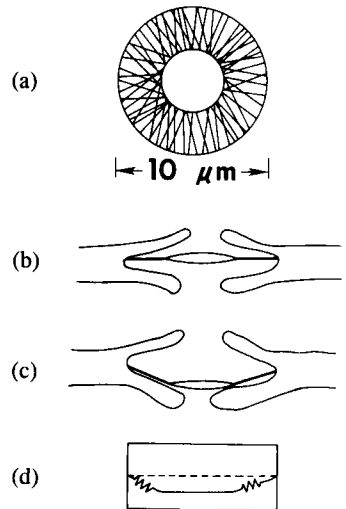


FIGURE 24.52 Schematic diagram of a bordered pit found in xylem tracheid cells. (a) Top view. The closing membrane is composed of a thick central region and a thin peripheral region. (b) Side view. A circular border arches over the pit cavity and contains the closing membrane. Pit is open. (c) Pit is closed. (d) Two-dimensional hydrodynamical model. (From Chapman *et al.*, 1977.) The dashed and solid lines represent initial and displaced positions respectively.

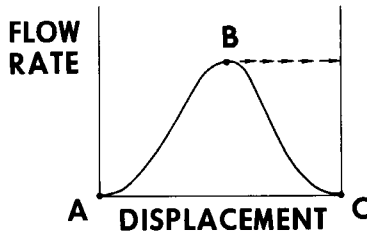


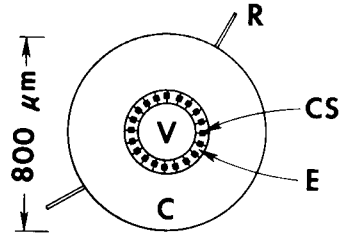
FIGURE 24.53 Results of the analysis of the model in Figure 24.52(d) (from Chapman *et al.*, 1977). Points *A* and *C* correspond to zero and maximum displacement respectively. As the flow rate is increased, the displacement of the membrane is increased until point *B*, after which the pit snaps shut (arrows). The equilibrium states on the curve *BC* are unstable.

Figure 24.53 shows the results of this analysis. It was found that for a given flow rate through the pit there are two equilibrium displacements, one stable and the other unstable. As the flow rate is increased to a value larger than the maximum permissible (see Fig. 24.53), the pit snaps shut. Thus, the pit functions as a valve to limit the flow rate in the xylem pathway.

A problem related to flow in the vascular system concerns observed daily changes in stem diameter accompanying changes in the rate of transpiration. The phenomenon is explained in terms of a decrease in the water content of cells near the xylem tissue resulting from an increase in the rate of transpiration. In order for the transpiration stream to flow, there must be a negative gradient in water potential from the roots to the leaves. This gradient reduces the value of the water potential at all points in the xylem (compared with values corresponding to zero transpiration). This, in turn, causes a decrease in water potential inside a typical cell near the xylem tissue throughout the stem and, accordingly, reduces the cell's turgor pressure and the associated elastic extension of the cell wall. As a result, the size of the cell and the diameter of the stem are decreased. Molz and Klepper (1972) studied this problem by assuming radial diffusion of water potential, a concept first discussed by Philip (1958a,b,c). They obtained good agreement with experimental observations and were able to explain an observed hysteresis loop in the stem diameter–leaf water potential relationship. Their work was extended by Parlange *et al.* (1975), who considered a variable diffusion coefficient and a corresponding nonlinear diffusion equation.

The flow of water in the parallel symplasm and apoplasm pathways has been described by a pair of coupled diffusion equations [Molz (1976), Molz and Ikenberry (1974), and Hornberger (1973)]. The coupling represents the flow between the symplasm and the apoplasm and depends upon various resistances in the model. Molz (1976) has applied these equations to a boundary-value problem representing the immersion of a sheet of tissue initially in equilibrium into a bath of pure water. Aifantis (1977) has decomposed the flow in the apoplasm into two components representing flow in the xylem vessels and flow in the cell walls. His treatment, based on the modern theory of continuum mechanics, neglects viscous effects and results in two coupled diffusion equations. Unger and Aifantis (1979) have applied this theory to a boundary-value problem representing flow in a cylindrical stem. Flow in the plasmodesmata of the symplasm has been studied by Blake (1978). An indi-

FIGURE 24.54 Schematic diagram of a transverse section of a root about one cm. from the root tip (after Nobel, 1974). *R* = root hair, *C* = cortex, *E* = endodermis, *CS* = casparian strip, and *V* = vascular tissue.



vidual plasmodesma has an internal diameter of about $0.05 \mu\text{m}$ and a length of about $1 \mu\text{m}$. Thus, the scale of this work is much smaller than many of the other problems considered in the biofluid mechanics of plants.

24.6.7 Flow in the Root

Figure 24.54 shows a schematic diagram of a transverse section of a root. Water is absorbed from the soil through the many root hairs (the presence of which greatly increases the absorbing surface area of the root) and flow radially inward across a region of storage tissue called the *cortex*, toward the xylem in the centrally located vascular tissue. Between the cortex and the vascular tissue, however, lies the endodermis, a single layer of cells that are separated from one another by an impermeable barrier called the *casparian strip*. Water must pass through the symplasm of the endodermal cells in order to enter the vascular tissue. Thus, the endodermis and casparian strip locally divide the apoplasm into two disconnected regions. Although the exact role of the endodermis is uncertain, it may function as a filter, selectively absorbing minerals, and it may be the site of observed changes in the plant's resistance to water flux, permitting absorption to occur more readily when the soil is less moist. Once the absorbed water reaches the xylem, it flows axially. See Newman (1976) for a summary of flow in the root.

Unlike the leaf, the root has received relatively little attention from fluid mechanicians. The usual approach has been to use a lumped system resistance–capacitance electric circuit analog [Seaton and Landsberg (1978)]. Although such models yield reasonable estimates for overall plant water fluxes, they do not take account of the geometry of the root. Of greater fluid mechanical interest are the following models, which involve a field-theory approach. Molz (1975) considered radial diffusive flow in a cylindrical root surrounded by a cylindrical region of soil. Continuity of water potential and of water flux were assumed at the soil–root interface. The study indicated that water potential gradients in the soil are small compared with those in the root, except under very dry soil conditions. Landsberg and Fowkes (1978) considered both radial absorption and axial diffusion of water along the length of a root. Their model predicted the value of the plant water potential at the base of the plant necessary to sustain a given flow rate through a root system with given characteristics. An expression was obtained for the optimal root length such that the overall root resistance to water is minimized. It is interesting to note that the mathematical statement of this problem is identical to that used to describe the assimilation of CO_2 in the intercellular air pathway of a leaf [Rand (1977a,b)].

24.6.8 Circumnutation

The phenomenon of *circumnutation* involves the circular motion of the stem of certain vine-like plants, providing them with a way to search for an external support to twine around. Experimental work on this problem goes back to Darwin (1865). Periods of oscillation have been found to range from one to twenty hours. Circumnutation is not a diurnal (daily) phenomenon, and it persists in the dark and in the gravity-free environment of the space shuttle [see Lubkin's (1992) thesis for references to the experimental literature]. Lubkin and Rand (1994) and Lubkin (1992, 1994) developed a mathematical model for circumnutation which involved reaction diffusion equations in the cross-section of the stem modeled as a hollow cylinder. The model supported waves of potassium concentration moving around the circumference of the stem, with water passively following the potassium ions. The side of the stem with high potassium ions would attract more water than the diametrically opposite side, and the corresponding unequal presence of water would cause the stem to bend. The model was used to study the *chirality* of circumnutation, i.e., the observed preference which many plants have to circumnutate in a preferred direction (i.e., clockwise versus counterclockwise).

24.6.9 Conclusions

As in other branches of biomechanics, research work on plants involves greater emphasis on modeling than does work in more traditional areas of mechanics. The researcher is presented with the biological description of the phenomenon to be studied and must invent an appropriate boundary-value problem to represent it. The modeling process has nothing like a unique solution, and the same physical problem can be treated in many different ways, each yielding some additional information. For example, the mesophyll cells in the interior of the leaf have been modeled by spheres [Rand and Cooke (1980) and Sinclair and Rand (1979)], by cylinders [Rand (1978b)], and by the exterior of a cylinder [Rand (1977a,b)]. The strategies encountered in biomechanical modeling involve a great deal of freedom of choice, more akin to sculpture or painting than to the traditional view of science.

Research work on biofluid mechanics of plants is by its nature interdisciplinary. The interaction between mechanics and fields such as agricultural engineering or plant physiology is essential, both to generate the relevant problems and to evaluate the significance of the solutions. In some cases, the use of a mathematical model has been particularly effective in a field where mathematical approaches are less common than experimental or descriptive methods. For example, the question of what makes a stomate open had been incorrectly attributed to differences in guard cell wall thickness prior to biomechanical analysis [Cooke *et al.* (1976)]. Also, the observed absence of evaporation from mesophyll cell walls inside the leaf had led to the conjecture that these walls were covered by waxy cuticle which retarded evaporation, an assumption which was shown to be unnecessary by use of a mathematical model [Rand (1977a,b)].

As we look towards the future of the study of the fluid mechanics of green plants, we hope for applications that permit plant breeders and geneticists to design plants which can withstand unusual stresses, such as frost and dehydrations. The ability to

1938 **FLUID DYNAMICS IN NATURE**

meaningfully incorporate into crop production considerations based on plant physiology will expand rapidly as the utility of mathematical models becomes more apparent to agriculturalists.

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