

FLUID MECHANICS OF GREEN PLANTS

Richard H. Rand

Department of Theoretical and Applied Mechanics, Cornell University,
Ithaca, New York 14853

INTRODUCTION

Why is the study of the biomechanics of green plants important? First, it has been estimated that plant life comprises 99% of the Earth's biomass (Bidwell 1974). Second, green plants are virtually the only ultimate source of food for animals through photosynthesis (the process of conversion of solar energy to stored chemical energy).

A biofluid-mechanical overview of a typical green plant is shown in Figure 1. See Nobel (1974) for an extensive self-contained quantitative introduction and order-of-magnitude analysis; for a shorter quantitative introduction, see Merva (1975). Meidner & Sheriff (1976) have written a short introduction that uses engineering concepts with a minimum of mathematics, and Canny (1977) has written a brief nonmathematical introduction for fluid mechanicians.

The leaves are the site of photosynthesis. This process requires sunlight, CO₂, and water, and produces glucose (a simple sugar) and oxygen. Sugars manufactured in the leaves are translocated to other parts of the plant via the vascular phloem tissue. Water and minerals absorbed in the roots are brought up to the leaves via the vascular xylem tissue. The upward xylem flow (called the transpiration stream) is driven by evaporation at the leaves, while the largely downward phloem flow is thought to be driven by concentration differences created locally by active transport (e.g. the Munch hypothesis; see Bidwell 1974).

Studies of each of these parts of the plant have involved special fluid mechanics problems based on the particular physiological function and geometry. This article introduces the reader to the concepts and problems

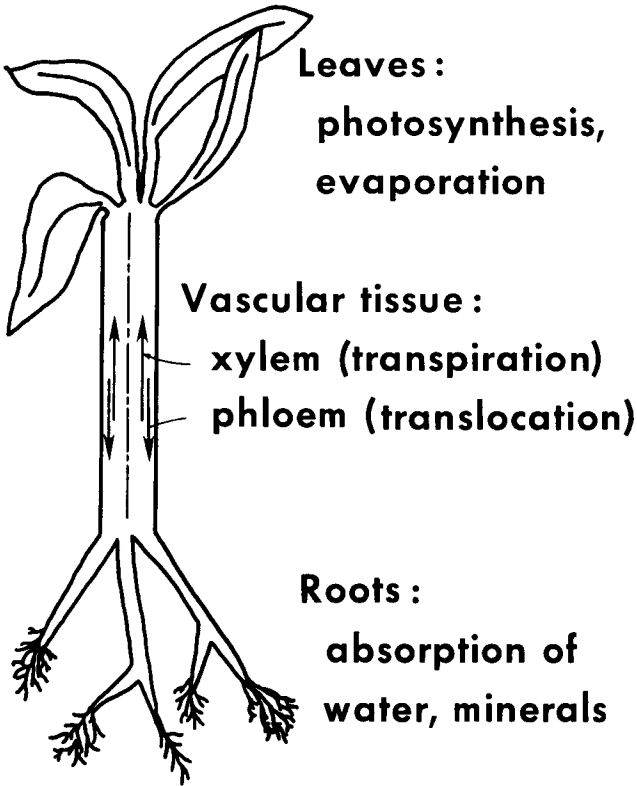


Figure 1 A biofluid-mechanical overview of a typical green plant.

that are unique to the fluid mechanics of plants and reviews the mathematical literature on this subject.

FLOW IN THE VASCULAR TISSUE

Let us compare the vascular system of plants with the more familiar human vascular system. In contrast to the human circulatory system, the vascular system of plants is open (Figure 1) and includes extensive branching at both the leaves and roots. Unlike the blood vessels of human physiology, the conduits of plants are formed of 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 (Figure 2) that die after reaching maturity, while the phloem contains sieve elements that remain metabolically active.

Blood vessels are often modeled as elastic tubes since their deformation may be significant due to the pulsatile nature of the flow. In plants, however, the flow is quasi-steady and the vascular cells (like all plant cells) have stiff cell walls, making a rigid-tube model appropriate. Reynolds numbers for flow in the human aorta and in the xylem of a plant are respectively about 2000 and 0.02 (see Table 1). This means that slow viscous (creeping) flow (Happel & Brenner 1965), in which the inertia terms are neglected in the Navier-Stokes equations, is a reasonable model for flow in the plant vascular system.

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.

The fluid mechanics of phloem flow has been considered by Rand & Cooke (1978) and Rand et al. (1980). As shown in Figure 2, 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 (Figure 3). The results of the analysis were compared with

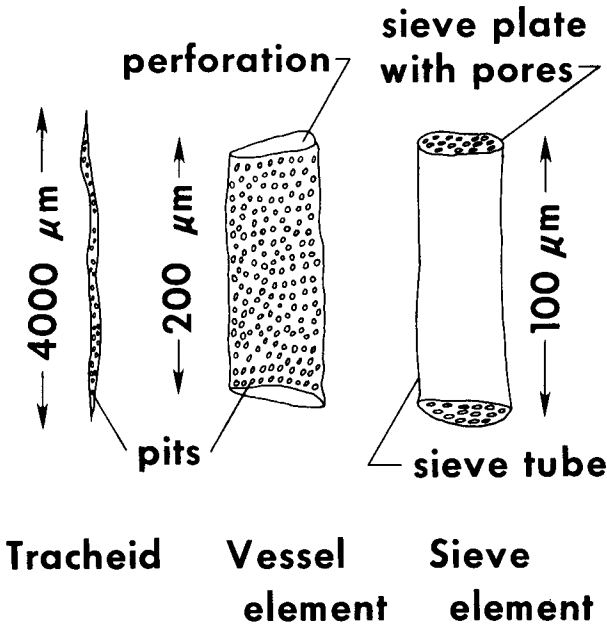


Figure 2 Fluid-conducting cells in the vascular tissue of plants (after Esau 1965). Tracheids and vessel elements are found in the xylem, while sieve elements are found in the phloem. Here and in the rest of this paper, the dimensions given are typical but do not represent statistical averages.

Table 1 Comparison of Reynolds numbers for flow in a xylem vessel and the human aorta

	Xylem vessel	Human aorta
Velocity U (cm/sec)	0.1	40
Radius R (cm)	0.002	1.5
Kinematic viscosity ν (cm ² /sec)	0.01	0.03
Reynolds number UR/ν	0.02	2000

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.

Let us now consider the flow in the xylem. Flow between two neighboring xylem tracheid cells occurs through pits (Figure 2). A typical bordered pit (Figure 4) consists of a circular border that arches over the pit cavity and contains a closing membrane. 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 5 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 Figure 5), the pit snaps shut. Thus the pit functions as a valve to limit the flow in the xylem pathway.

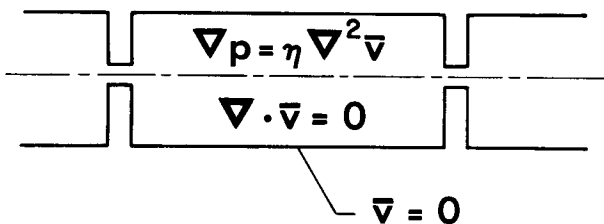


Figure 3 Axisymmetric single-pore model of flow in a sieve element of the phloem tissue (Rand & Cooke 1978). The field equations correspond to the steady creeping motion of an incompressible fluid.

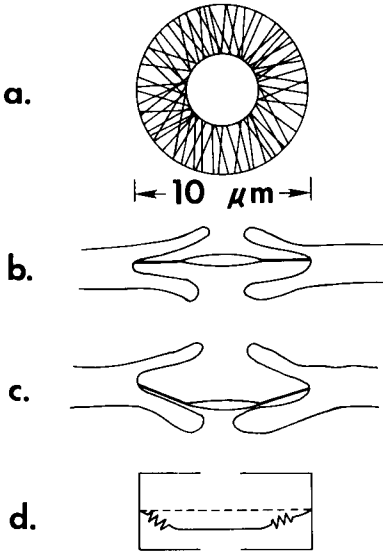


Figure 4 Schematic diagram of a bordered pit found in xylem tracheid cells. (a) Top view. The closing membrane is composed of a thick central region and a thin peripheral region. (b) Side view. A circular border arches over the pit cavity and contains the closing membrane. Pit is open. (c) Pit is closed. (d) Two-dimensional hydrodynamical model (Chapman et al. 1977). The dashed and solid lines represent initial and displaced positions respectively.

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 to understand this problem, we must consider the concept of water potential.

Water in plants moves 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, the water potential ψ (Nobel 1974):

$$\psi = p - RTc + \rho gz, \tag{1}$$

where

p = hydrostatic pressure (bar),

R = gas constant = $83.141 \text{ cm}^3\text{-bar/mole K}$,

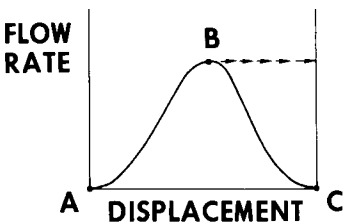


Figure 5 Results of the analysis of the model in Figure 4d (Chapman et al. 1977). Points A and C correspond to zero and maximum displacement respectively. As the flow rate is increased, the displacement of the membrane is increased until point B, after which the pit snaps shut (arrows). The equilibrium states on curve BC are unstable.

T = temperature (K),

c = concentration of all solutes in assumed dilute solution (mole/cm³),

ρ = density of water (g/cm³),

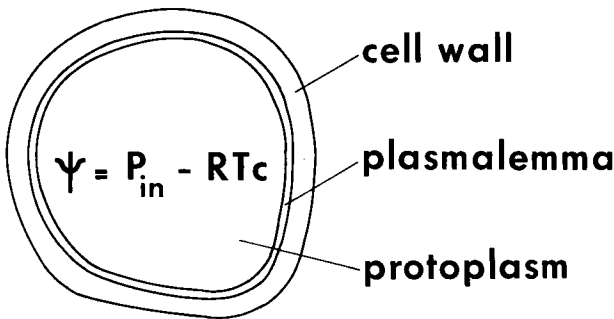
g = acceleration of gravity = 980 cm/sec²,

z = height (cm).

Here ψ is in bars, a convenient unit commonly used in plant studies for measuring pressure. One bar equals 10⁶ dyne/cm² 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 (Figure 6). 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 the exterior of the cell, the hydrostatic pressure inside the cell can be larger than that outside the cell [from Equation (1)]. 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" pressure inside the cell.

Let us return now to the problem of the daily changes in stem diameter due to dehydration during 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



$$\Psi = P_{out} < P_{in}$$

Figure 6 Schematic diagram of a typical plant cell. For equilibrium, the water potentials ψ inside and outside the cell must be equal.

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 & 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.

A related and important concept 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 & Sheriff 1976, p. 51).

The flow of water in the parallel symplasm and apoplasm pathways has been described by a pair of coupled diffusion equations (Molz 1976; see also Molz & Ikenberry 1974 and Molz & 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 & 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 individual plasmodesma has an internal diameter of about $0.05 \mu\text{m}$ and a length of about $1 \mu\text{m}$. This work represents the smallest scale yet considered in the biofluid mechanics of plants.

FLOW IN THE LEAF

The structure of the leaf can be explained in terms of its function. The thinness of the leaf enables CO_2 to diffuse from the ambient atmosphere into the leaf interior, where it is utilized in photosynthesis in the chloroplasts of the mesophyll cells (Figure 7). The familiar branching pattern of the vascular tissues in the leaf serves to irrigate the mesophyll cells in order to replace water that has been lost through evaporation. Water loss is generally thought to be undesirable, especially in times of drought (although the cooling effect of evaporation may be of significant value). The outer layer of leaf cells (the epidermis; see Figure 7) is covered with a layer of waxy material called cutin that tends to prevent water loss.

CO_2 and water vapor respectively enter and leave the leaf through small holes in the epidermis called stomata (Meidner & Mansfield 1968). An individual stomate is composed of two specialized guard cells (Figure 8) which, through their elastic deformation under hydrostatic loading, can affect the width of the stomatal pore. Thus stomata can act like valves to limit water loss when CO_2 is not needed for photosynthesis. For example, stomata are generally closed at night when the absence of sunlight prevents photosynthesis.

Cooke et al. (1976) have considered the elastostatics of a stomatal guard cell by using a linear anisotropic thin-shell model and a finite-element analysis. An increase in hydrostatic pressure in the guard cell tended to open the stomatal pore, while an increase in neighboring subsidiary cell pressure tended to close the pore. It was shown that the elliptic shape of the stomate (Figure 8*a, b*) is critical for opening and that other features (such as wall thickening and radial stiffening) could help the opening process, but were not essential. In particular, it was shown analytically that a circular torus model would close rather than open

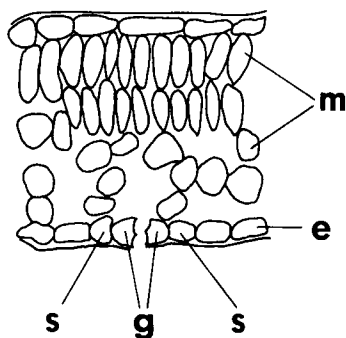


Figure 7 Schematic diagram of a transverse section of a leaf (after Nobel 1974). A representative value for leaf thickness is $300\ \mu\text{m}$. (m) mesophyll cell, (e) epidermal cell, (g) guard cell, (s) subsidiary cell.

upon inflation. This work was extended by Cooke et al. (1977) to include nonlinear effects.

The flow of water along the transpiration stream in the leaf proceeds through the branching xylem system to the xylem termini, and then continues through the apoplastic mesophyll cell walls to those mesophyll cells near the stomatal pore where evaporation occurs. Stroshine et al. (1979) have studied flow in the leaf xylem. 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 intermediate and small bundles.

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 μm (Nobel 1974, p. 51). The pressure difference across a spherical meniscus is given by

$$\Delta p = 2\sigma/r, \tag{2}$$

where

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

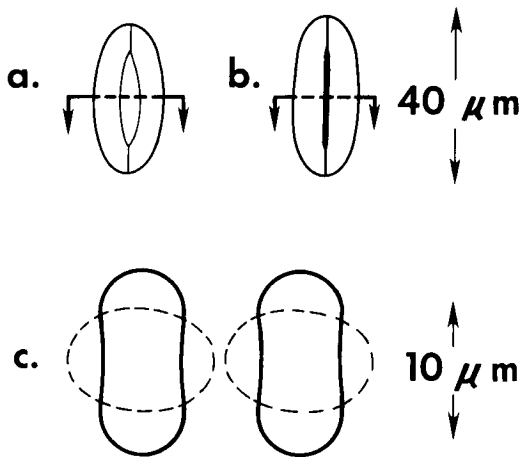


Figure 8 Schematic diagram of an elliptical stomate. (a) View looking onto the leaf surface. Pore open. (b) Pore closed. (c) Transverse view of finite-element model of two guard cells (Cooke et al. 1976). Note the change of scale. Dashed and solid curves represent initial and deformed configurations respectively.

Here Δp is about 300 bars, and since one bar is equal to a gravitational head of about ten meters, this effect accounts 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 & Scholander 1976, p. 18; Nobel 1974, p. 52), the presence of small air bubbles and other imperfections reduces the observed tensile strength in laboratory experiments. Nevertheless, the plant is evidently able to grow a vascular system relatively free from air bubble defects.

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.

Gaseous Diffusion

The evaporating water proceeds by gaseous diffusion through the stomatal pore (if it is open), through a still air layer adjacent to the leaf, and into the ambient atmosphere. In a similar fashion, CO_2 diffuses into the leaf interior where it is absorbed into the wet mesophyll cell walls. Gaseous diffusion in the leaf has received a great deal of attention since it was first studied from a mathematical point of view by Brown & Escombe (1900). By modeling the leaf surface as a plane septum with a circular hole and the pore as a circular cylinder, they were able to explain the experimentally observed relatively large rates of transpiration from leaves (comparable to evaporative fluxes from an equal-sized body of water). A recent review of leaf diffusion models (Cooke & Rand 1980) contains many references in addition to those that follow.

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) considered the interaction effects between neighboring stomatal pores. Using separation of variables, he showed that the flux

depends on both the spacing between stomata on the leaf surface and the boundary-layer thickness. Substantial increases in flux due to interaction effects could occur for closely spaced stomata with a relatively thin boundary layer.

Holcomb & Cooke (1977) extended this work 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-layer thickness, and pore depth.

Parlange & Waggoner (1970) used conformal mapping to study diffusion through a two-dimensional slit. They compared their results with the formula of Brown & Escombe (1900) and found the latter to be most accurate for thin, deep slits.

Current treatments of gaseous diffusion in the leaf (see, for example, Nobel 1974) 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. 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%.

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.

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.

The gaseous diffusion of water vapor and CO_2 differ in one important respect: although the CO_2 diffuses into the deep interior of the leaf to be absorbed by the mesophyll cells, several independent experimental investigations have shown that water vapor evaporates only from those cell walls near the stomatal pore (Tyree & Yianoulis 1980). This phenomenon has been explained by considering the physical chemistry of equilibrium between the liquid and gaseous phases at the cell wall (Rand 1977a,b). Since the cell-wall liquid is a dilute solution in which CO_2 is the solute and water the solvent, CO_2 satisfies Henry's law while water vapor satisfies Raoult's law. When stated as boundary conditions for the diffusion problem, these principles give substantially different predic-

tions for CO_2 and water vapor, in qualitative agreement with the experimental observations. In related work, the diffusion of CO_2 in sun versus shade (i.e. thick versus thin) leaves was studied by Rand (1978b).

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 & 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 & 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.

Stomatal Oscillations

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 & 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 acts like a feedback element and is responsible for the oscillation, which 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 (Cooke et al. 1976). 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 (Figure 9).

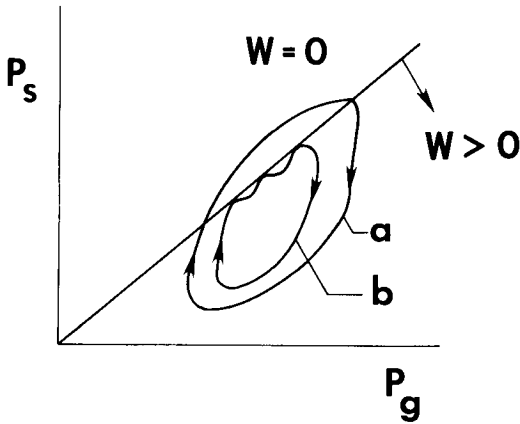


Figure 9 Limit cycles representing stomatal oscillations in the p_g - p_s plane. Here p_g and p_s represent hydrostatic pressures in guard and subsidiary cells respectively, and w represents pore width. The region above the straight line corresponds to a closed pore ($w = 0$). Arrow shows direction of increasing pore width. (a) Stomatal oscillation due to hydraulic feedback loop only (Delwiche & Cooke 1977). (b) Stomatal oscillation due to both hydraulic and CO_2 feedback effects (Upadhyaya et al. 1980a,b).

This work was extended by Rand et al. (1981) by embedding the original system of Delwiche & 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 (Figure 10). The system was shown to contain a Hopf bifurcation (Marsden & McCracken 1976) 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 & 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.

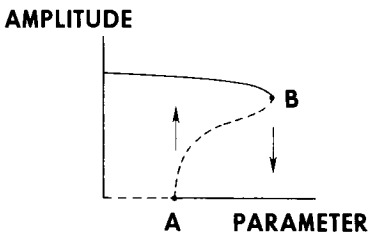


Figure 10 Changes in the amplitude of the stomatal oscillation of Figure 9a due to changes in a system parameter (Rand et al. 1981). Zero amplitude corresponds to equilibrium behavior. The dashed and solid lines correspond to unstable, and stable motions respectively. At point A an unstable equilibrium 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.

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 (Figure 9), in agreement with the experimental observations of other investigators.

In order to explore the effects of coupling between neighboring stomata, Rand et al. (1982) studied a model of the dynamics of a system of N coupled stomatal oscillators. This work was based on the possibility that even on the same leaf, some stomata may be open while others are closed. Although in principle one may envision *waves* of stomatal-opening moving across the leaf surface, analysis of the model predicted that for a wide range of parameter values a uniform leaf would exhibit a stable, spatially uniform, synchronized behavior.

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 atmospheric conditions. However, this savings in moisture content occurs at the expense of a reduction in the CO_2 assimilation rate.

FLOW IN THE ROOT

Although we are concerned only with the role of the root as an organ for absorbing water and minerals from the soil, note that the root also serves to store carbohydrates and to anchor the plant in the soil.

Figure 11 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 flows 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 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.

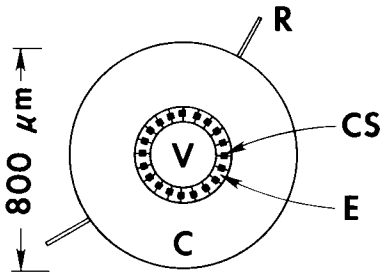


Figure 11 Schematic diagram of a transverse section of a root about one cm from the root tip (after Nobel 1974). (R) root hair, (C) cortex, (E) endodermis, (CS) casparian strip, (V) vascular tissue.

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 (see, for example, Seaton & 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 & 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).

CONCLUDING REMARKS

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.

Moreover the work 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.

Finally, we note that a glance at the contents of a current biomechanics journal or conference reveals that almost all the research work concerns animal systems, and most of that the human body. In view of the importance of plants to our planet and to our society, we might ask why the biomechanics of plants has received so little attention. Perhaps it is a case of chauvinism by species; work by our species has proceeded most rapidly on biological systems most similar to ourselves, and plants are very different. In any case it is clear that the body of knowledge of biomechanics, a relatively new field, is still developing new branches and we expect to see more attention given to the study of plants in the future.

Literature Cited

- Aifantis, E. C. 1977. Mathematical modeling for water flow in plants. In *Proc. 1st Int. Conf. Math. Modeling, Rolla, Mo.*, ed. X. J. R. Avula, 2:1083-90
- Bange, G. G. J. 1953. On the quantitative explanation of stomatal transpiration. *Acta Bot. Neerl.* 2:255-97
- Bidwell, R. G. S. 1974. *Plant Physiology*. New York: MacMillan
- Blake, J. R. 1978. On the hydrodynamics of plasmodesmata. *J. Theor. Biol.* 74:33-47
- Brown, H. T., Escombe, F. 1900. Static diffusion of gases and liquids in relation to the assimilation of carbon and translocation in plants. *Philos. Trans. R. Soc. London Ser. B* 193:223-91
- Canny, M. J. 1977. Flow and transport in plants. *Ann. Rev. Fluid Mech.* 9:275-96
- Chapman, D. C., Rand, R. H., Cooke, J. R. 1977. A hydrodynamical model of bordered pits in conifer tracheids. *J. Theor. Biol.* 67:11-24
- Cooke, J. R. 1967. Some theoretical considerations in stomatal diffusion: a field theory approach. *Acta Biotheor.* 17:95-124
- Cooke, J. R. 1969. The influence of stomatal spacing upon diffusion rate. *ASAE Pap. No. 69-525*. Am. Soc. Agric. Eng., St. Joseph, Mich.
- Cooke, J. R., Debaerdemaeker, J. G., Rand, R. H., Mang, H. A. 1976. A finite element shell analysis of guard cell deformations. *Trans. ASAE* 19:1107-21
- Cooke, J. R., Rand, R. H. 1980. Diffusion resistance models. In *Predicting Photosynthesis for Ecosystem Models*, ed. J. D. Hesketh, J. W. Jones, 1:93-121. Boca Raton, Fla: CRC Press
- Cooke, J. R., Rand, R. H., Mang, H. A., Debaerdemaeker, J. G. 1977. A nonlinear finite element analysis of stomatal guard cells. *ASAE Pap. No. 77-5511*. Am. Soc. Agric. Eng., St. Joseph, Mich.
- Delwiche, M. J., Cooke, J. R. 1977. An analytical model of the hydraulic aspects of stomatal dynamics. *J. Theor. Biol.* 69:113-41
- Esau, K. 1965. *Plant Anatomy*. New York: Wiley
- Gross, L. J. 1981. On the dynamics of internal leaf carbon dioxide uptake. *J. Math. Biol.* 11:181-91
- Hammel, H. T., Scholander, P. F. 1976. *Osmosis and Tensile Solvent*. New York: Springer
- Happel, J., Brenner, H. 1965. *Low Reynolds Number Hydrodynamics*. Englewood Cliffs, NJ: Prentice Hall
- Holcomb, D. P., Cooke, J. R. 1977. An electrolytic tank analog determination of stomatal diffusion resistance. *ASAE Pap. No. 77-5510*. Am. Soc. Agric. Eng., St. Joseph, Mich.
- Landsberg, J. J., Fowkes, N. D. 1978. Water movement through plant roots. *Ann. Bot.* 42:493-508
- Marsden, J. E., McCracken, M. 1976. *The Hopf Bifurcation and its Applications*. New York: Springer
- Meidner, H., Mansfield, T. A. 1968. *Physiology of Stomata*. New York: McGraw-Hill
- Meidner, H., Sheriff, D. W. 1976. *Water and Plants*. New York: Wiley
- Merva, G. E. 1975. *Physioengineering Principles*. Westport, Conn: AVI Publ.
- Molz, F. J. 1975. Potential distributions in the soil-root system. *Agron. J.* 67:726-29
- Molz, F. J. 1976. Water transport through plant tissue: the apoplasm and symplasm pathways. *J. Theor. Biol.* 59:277-92
- Molz, F. J., Hornberger, G. M. 1973. Water transport through plant tissues in the presence of a diffusible solute. *Soil Sci. Soc. Am. Proc.* 37:833-37

- Molz, F. J., Ikenberry, E. 1974. Water transport through plant cells and cell walls: theoretical development. *Soil Sci. Soc. Am. Proc.* 38:699-704
- Molz, F. J., Klepper, B. 1972. Radial propagation of water potential in stems. *Agron. J.* 64:469-73
- Newman, E. I. 1976. Water movement through root systems. *Philos. Trans. R. Soc. London Ser. B* 273:463-78
- Nobel, P. S. 1974. *Introduction to Biophysical Plant Physiology*. San Francisco: Freeman
- Parkhurst, D. F. 1977. A three-dimensional model for CO₂ uptake by continuously distributed mesophyll in leaves. *J. Theor. Biol.* 67:471-88
- Parlange, J. Y., Turner, N. C., Waggoner, P. E. 1975. Water uptake, diameter change, and nonlinear diffusion in tree stems. *Plant Physiol.* 55:247-50
- Parlange, J. Y., Waggoner, P. E. 1970. Stomatal dimensions and resistance to diffusion. *Plant Physiol.* 46:337-42
- Philip, J. R. 1958a. The osmotic cell, solute diffusibility, and the plant water economy. *Plant Physiol.* 33:264-71
- Philip, J. R. 1958b. Propagation of turgor and other properties through cell aggregations. *Plant Physiol.* 33:271-74
- Philip, J. R. 1958c. Osmosis and diffusion in tissue: half-times and internal gradients. *Plant Physiol.* 33:275-78
- Rand, R. H. 1977a. Gaseous diffusion in the leaf interior. *Trans. ASAE* 20:701-4
- Rand, R. H. 1977b. Gaseous diffusion in the leaf interior. In *1977 Biomech. Symp.*, ed. R. Skalak, A. B. Schultz, 23:51-53
- Rand, R. H. 1978a. The dynamics of an evaporating meniscus. *Acta Mech.* 29:135-46
- Rand, R. H. 1978b. A theoretical analysis of CO₂ absorption in sun versus shade leaves. *J. Biomech. Eng. Trans. ASME* 100:20-24
- Rand, R. H., Cooke, J. R. 1978. Fluid dynamics of phloem flow: an axisymmetric model. *Trans. ASAE* 21:898-900, 906
- Rand, R. H., Cooke, J. R. 1980. A comprehensive model for CO₂ assimilation in leaves. *Trans. ASAE* 23:601-7
- Rand, R. H., Storti, D. W., Upadhyaya, S. K., Cooke, J. R. 1982. Dynamics of coupled stomatal oscillators. *J. Math. Biol.* In press
- Rand, R. H., Upadhyaya, S. K., Cooke, J. R. 1980. Fluid dynamics of phloem flow. II. An approximate formula. *Trans. ASAE* 23:581-84
- Rand, R. H., Upadhyaya, S. K., Cooke, J. R., Storti, D. W. 1981. Hopf bifurcation in a stomatal oscillator. *J. Math. Biol.* 12:1-11
- Seaton, K. A., Landsberg, J. J. 1978. Resistance to water movement through wheat root systems. *Aust. J. Agric. Res.* 29:913-24
- Sinclair, T. R., Goudriaan, J., Dewit, C. T. 1977. Mesophyll resistance and CO₂ compensation concentration in leaf photosynthesis models. *Photosynthetica* 11:56-65
- Sinclair, T. R., Rand, R. H. 1979. Mathematical analysis of cell CO₂ exchange under high CO₂ concentrations. *Photosynthetica* 13:239-44
- Stroshine, R. L., Cooke, J. R., Rand, R. H., Cutler, J. M., Chabot, J. F. 1979. Mathematical analysis of pressure chamber efflux curves. *ASAE Pap. No. 79-4585*. Am. Soc. Agric. Eng., St. Joseph, Mich.
- Thornley, J. H. M. 1976. *Mathematical Models in Plant Physiology*. New York: Academic
- Tyree, M. T., Yianoulis, P. 1980. The site of water evaporation from sub-stomatal cavities, liquid path resistances and hydroactive stomatal closure. *Ann. Bot.* 46:175-93
- Unger, D. J., Aifantis, E. C. 1979. Flow in stems of plants. In *Proc. 3rd Eng. Mech. Div. Specialty Conf. ASCE*, Austin, Tex., pp. 501-4
- Upadhyaya, S. K., Rand, R. H., Cooke, J. R. 1980a. Stomatal dynamics. In *1980 Advances in Bioengineering*, ed. V. C. Mow, pp. 185-88. New York: ASME
- Upadhyaya, S. K., Rand, R. H., Cooke, J. R. 1980b. A mathematical model of the effects of CO₂ on stomatal dynamics. *ASAE Pap. No. 80-5517*. Am. Soc. Agric. Eng., St. Joseph, Mich.
- Upadhyaya, S. K., Rand, R. H., Cooke, J. R. 1981. The role of stomatal oscillations on plant productivity and water use efficiency. *ASAE Pap. No. 81-4017*. Am. Soc. Agric. Eng., St. Joseph, Mich.
- Webster, I. A. 1981. The use of the effectiveness factor concept in CO₂ diffusion in the leaf interior. *Ann. Bot.* 48:757-60