

Shell analysis of elliptical guard cells in higher plants: a review

J. Robert COOKE*, Richard H. RAND, Herbert A. MANG, Josse G. DeBAERDEMAEKER, Jae Young LEE

*Professor Emeritus, Department of Biological and Environmental Engineering
214 Riley-Robb Hall, Cornell University, Ithaca, NY 14853 USA
jrc7@cornell.edu and j_robert_cooke@mac.com

Abstract

This presentation reviews finite element shell analyses (linear and nonlinear, isotropic and anisotropic) of microscopic stomata modeled as doubly-elliptic toroidal shells. Stomata are the regulating valve in the seminal issue of water and carbon dioxide transport in plant biology. The finite element method allows more realistic modeling of complex geometries and material properties that are common in biology.

1. Introduction

The physical sciences and engineering are increasingly broadening their traditional focus to include topics formerly within the exclusive domain of the biological sciences. Biological organisms, of course, are governed by and must function within the constraints of physics, so this expansion is direct. As the tools of engineering evolve and mature, especially the digital computer and software implementations such as the finite element method, the opportunities for cross-fertilization between the physical and biological domains increase. We hope that this presentation will encourage other attendees of this conference to turn their attention to the study of biology and to the transfer of the insights gained and methods developed in the physical sciences.

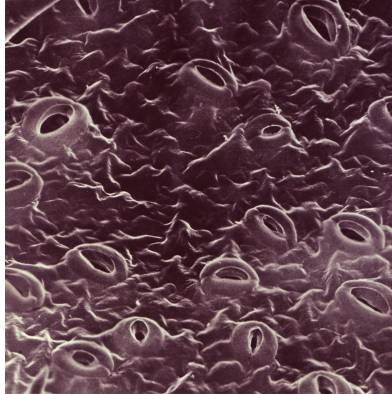
This presentation will review an application in plant physiology – an area that has attracted far less attention to date than has been the case for biomedical studies and animal physiology. The finite element method makes it feasible to deal effectively with the typical biological circumstances of increased geometrical complexity and highly anisotropic and nonlinear material properties and composites. Our focus will be on the surprisingly deep insights derived from studies of 30 and 20 years ago (Cooke et al. [1, 2] and Lee [4]).

Our efforts utilized software, FESIA, being developed at the time by Richard Gallagher and colleagues (Thomas and Gallagher [5]) here at Cornell in structural engineering. Their interest had been motivated by some rather dramatic collapses in multi-story tall concrete structures coming into usage at that time as cooling towers. They had developed a shell element that would accommodate a doubly curved surface such as occurs in a hyperbolic paraboloid. As an illustration of the theme of this conference, they were interested in a megastructure and we were interested in a structure of microscopic dimensions, i.e., invisible to the unaided eye. One other important attribute deserves mention at the outset: The system we are studying already exists and is functioning. Our interest primarily is one of reverse engineering, i.e. analysis rather than design.

2. Background

2.1 Plant biology considerations: Our project sought to understand better the processes of carbon dioxide and water exchange between plants and the environment, especially for agronomically important crops, that through evolution developed an effective feedback control system for regulating this gas exchange process. Higher plants provide an internal environment in which the energy received from the sun is converted into energy usable by the plant. That process, called photosynthesis, requires a source of carbon, which is obtained from the carbon dioxide in the atmosphere. Terrestrial plants are able to avoid desiccation in a relatively dry environment as a consequence of a relatively impervious outer surface. In many respects this is analogous to the thermal

environment provided by a building's outer surfaces. Passage of carbon dioxide into the plant's interior is facilitated by specialized passages analogous to windows that are opened and closed by the plant.



Specialized epidermal cells on plants, called guard cells, form pores called stoma that open and close (Figure 1) acting as an actuator valve for the passage of gases between the plant's interior and its environment. Usually these pores are open during the daylight when photosynthesis can proceed, and closed at night, blocking gas exchange. Because the plant's interior is water vapor saturated and therefore at higher concentration than the ambient environment, any time stomata are open for carbon dioxide uptake, water vapor moves in the opposite direction through the same pathway.

Figure 1. Fully opened stomata on lower surface of a cucumber leaf. (from Troughton and Donaldson [6])

One of the two most common geometrical shapes for stomata consists of a pair of kidney-shaped cells which we modeled as an elliptical torus, i.e., as a torus that is elliptical in plan view as seen from the outer surface of the leaf, and also elliptical in elevation view. The opening and closing of the pore was conjectured as early as 1856 to result from opposing forces caused by hydrostatic pressures inside the guard cell and from the adjacent cells.

Before the emergence of digital computers and the finite element method, only less realistic modeling of the behavior of the mechanics of the opening and closing of the pore was possible. Various beam theories were applied, but offered little understanding of the process by which pores opened. Two of the present authors (Rand and Cooke) applied Flügge's (then) recent thin shell theory of a circular torus with disappointing results. Namely, a circular torus of biologically realistic dimensions, when inflated, causes the pore size to decrease, rather than increase. Such behavior would be catastrophic for a plant – the pore must open when water is in ample supply (when some water loss can be tolerated) and close when water is in short supply (flaccid guard cells). (Note: An unphysiological garden hose shape when joined end-to-end and inflated would exhibit an increasing 'pore'.) This suggested that the observed non-circular shape of stomata played an essential role in their functioning as valves. However, since no analytical solution was available, it was natural to utilize the finite element method to study their behavior.

2.2 Shell considerations Figure 2 shows two views of the doubly elliptical shell studied, which includes a plate at each end of the guard cell pair. This plate does limit the outward expansion of the shell at each end of the pair, but is not required for the pore to open when the internal pressure is increased. Geometrical nonlinear aspects reveal some additional properties. One of the authors (Mang) generalized the FESIA software to handle geometric nonlinearities. Unsurprisingly, the nonlinear studies revealed that there are limits to the size of the pore opening as a result of increases in guard cell pressure. That is, the pore cannot be made arbitrarily large. Indeed, as the circular model showed, a contrary behavior would be expected as a more circular geometry is approached. Mang also generalized the FESIA software to include orthogonally anisotropic material properties so that we could model the role of the micellae (radially oriented microfibrils). A new finite element for shell analysis was introduced by Lee in 1986 and used in the subsequent calculations.

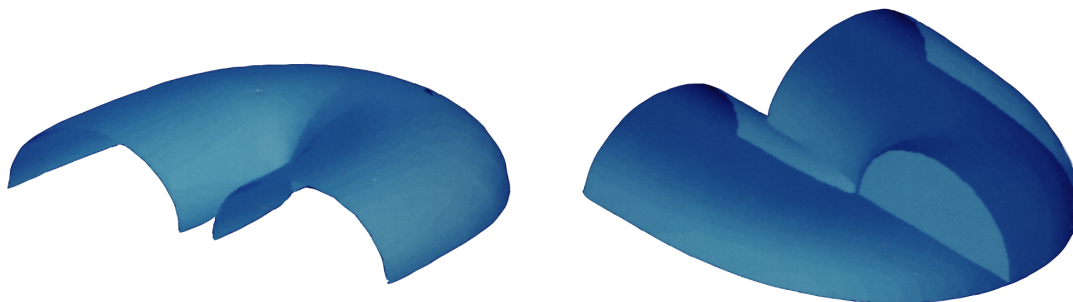
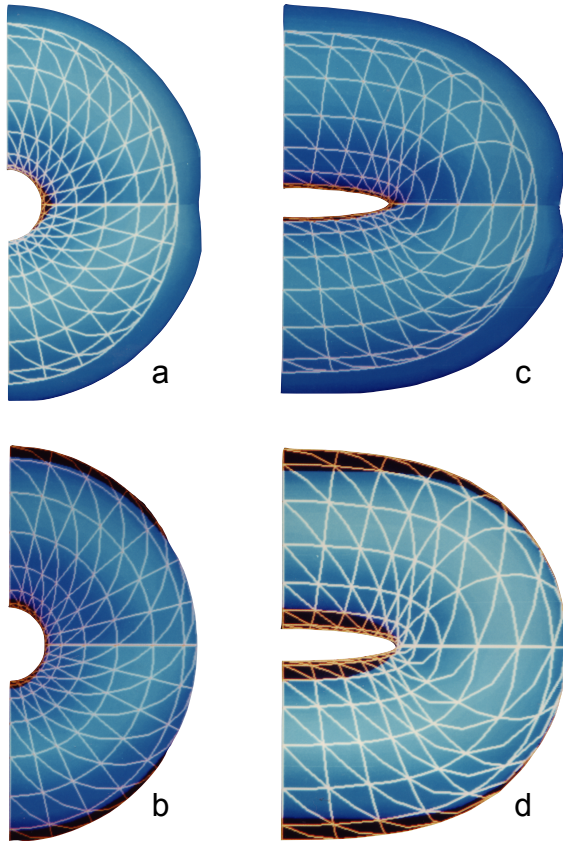


Figure 2. Toroidal shell – elliptical in plan and elevation views. Bottom view at right shows the plate at the end. From Lee [4].

3. Results

The elliptical geometry is the fundamental attribute governing the mechanism of pore opening! Nowhere in the plant kingdom does a circular stoma exist. That shape simply would not operate correctly.



Only half of a guard cell is shown in Figure 3. *Elevation views:* The top row has circular and the bottom elliptical cross sections. *Plan views:* The left column has circular and the right one elliptical top views.

Figure 3. Four geometrical shapes: a) circular torus (plan and elevations) with plate in end, b) circular torus (plan view) elliptical in elevation with plate in end, c) elliptical torus (plan view) circular in elevation with plate at end, d) elliptical in plan view and elliptical in elevation (without end plate) From Lee [4].

A circular torus with a circular cross section (a) would disturb the adjacent epidermal surface and the pore would not open. When the elevation cross section is made elliptical (b) the disturbance to the adjacent leaf surface is less, but the pore does not open sufficiently when inflated. If the top (or plan) cross section is made elliptical (c), but the elevation cross section remains circular, the adjacent cells would be disturbed and the pore would be little influenced by pressurization of the guard cell. Finally, when the torus (d) is doubly elliptical – plan and elevation – the guard cell does not bulge into the adjacent cells of the leaf surface and the pore width increases (moving in a direction opposite to the internally applied pressure).

Figure 4 shows the deformed shape of a doubly-elliptical toroidal shell. The shape of the deformed elliptical torus reveals another attribute of importance that has previously been ignored. Namely, when inflated, the shell expands mostly vertically (out of the plane of the leaf surface), minimizing the stretching of the leaf surface.

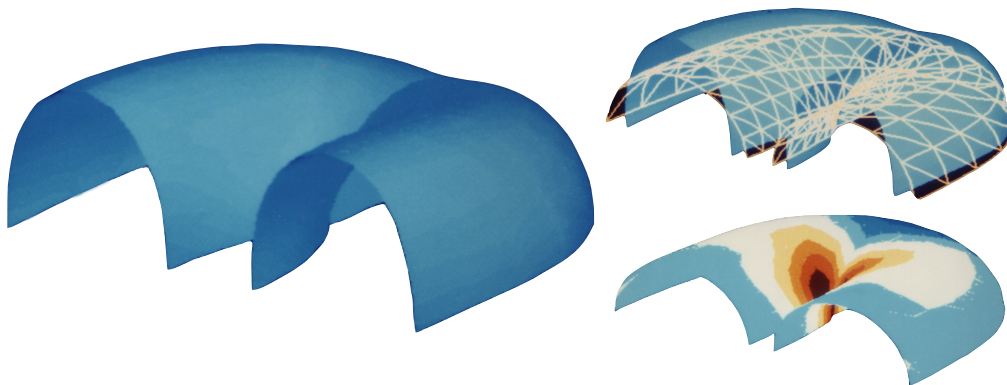
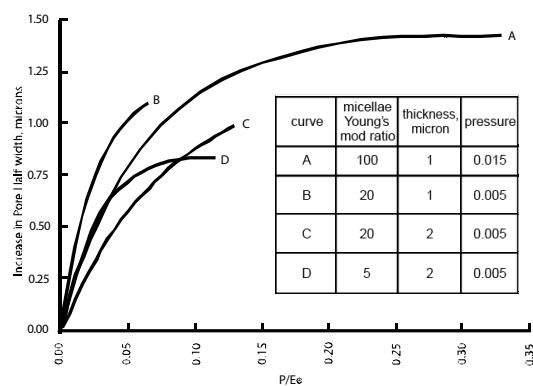
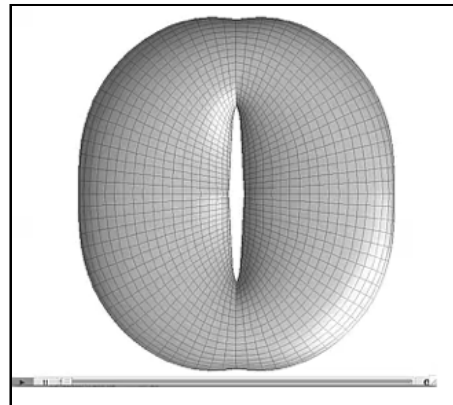


Figure 4 shows the deformed shape for an elliptical torus having an elliptical elevation cross section and end plate. Top-right shows the deformed shape superimposed on the mesh. Bottom-right shows the major principal stresses at the middle surface. From Lee [4].

The shell model did not impose a constraint on the length of the pore but that movement is inherently negligible, as reported in the experimental literature and confirmed by both the linear and nonlinear analyses.

Prior to our work, the two prevailing theories of the mechanics of pore opening attributed the response to 1) a thicker ventral wall of the guard cell (facing the pore) than occurs for the opposite guard cell wall (facing the surrounding cells) and 2) the presence of radial cellulose microfibrils in the guard cell, resulting in anisotropic material properties. Our finite element analyses showed that a) the dominant consideration is geometry, b) a perfectly uniform wall thickness for a doubly-elliptical shell will work correctly, and c) a perfectly isotropic elliptical torus will open under static pressure when inflated BUT the anisotropic property becomes a decided advantage when the dynamical response of the feedback control system is considered. Specifically, the internal volume (lumen) of the guard cell is much smaller than the enclosed volume of the surrounding cells so when a unit of water diffuses from the larger volume into the smaller volume, the pressure drop in the surrounding volume is less than the pressure increase in the smaller volume. Hence, the radial stiffening allows a smaller external pressure change to offset a larger pressure change inside the guard cell.

That is, in general, an increase in internal pressure opens the pore while a smaller increase in the surrounding pressure is able to counteract and close the pore. Indeed, the pore width can be represented as a multilinear function of the internal pressure and the pressure in the adjacent cell. This result is consistent with two very different experimental approaches: 1) pressurized inflation of the guard cell with the surrounding cells ruptured and pressuration of the surrounding cells with the guard cell ruptured, and 2) a plasmolytic approach in which osmotic conditions were used to alter the pressures. (A subsequent study of the dynamics of pore opening (Delwiche and Cooke [3]) revealed that this relationship must be clipped to exclude negative pore widths and that this is the key issue in causing a stable oscillatory behavior (a limit cycle) for stomata under drought stress.) (Double-click to see the animation at right.)



The pore width rises in a nonlinear manner and plateaus with increasing pressure, i.e., the width cannot be increased arbitrarily. Decreasing the wall thickness increases the pore size for a given pressure. The greater the stiffness provided by the micellae, the greater the maximum pore width achievable. However, most of the diffusive control is achieved with smaller pore widths, making larger widths unnecessary.

Figure 5 Pore width vs normalized internal pressure for the nonlinear model (Cooke et al. [2].)

References

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