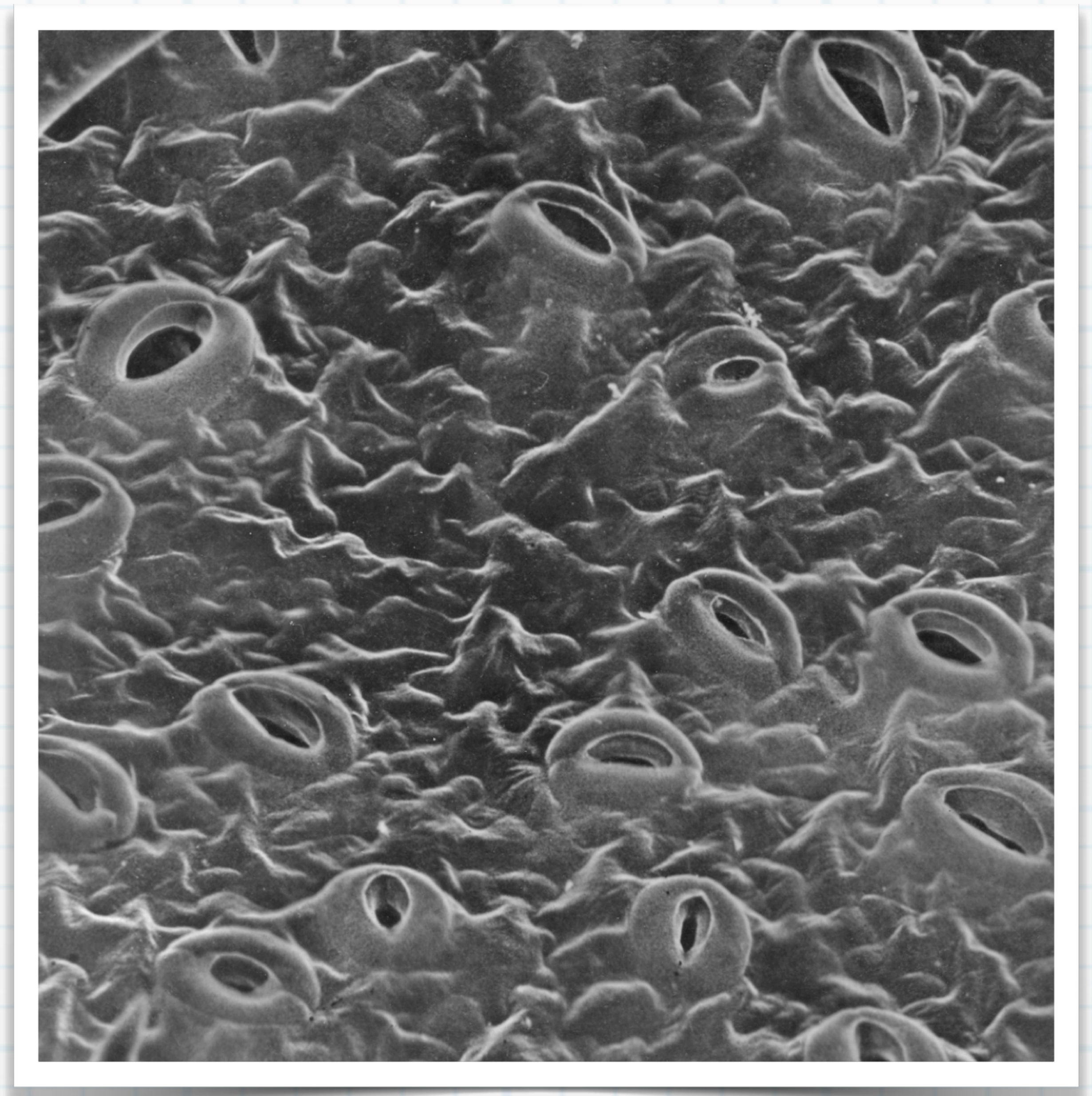
Stomatal Response

An Overview Book for Plant Scientists



J. Robert Cooke

November 10, 2023

A Professorial Postscript Lecture

Active Participants in the Plant Biomechanics Group at Cornell University

* J. R. Cooke
* J. G. DeBaerdemaker
* M. J. Delwiche
* D. P. Holcomb
* J. Y. Lee
* H. A. Mang
* R. H. Rand
* N. S. Scott
* E. T. Sobel
* D. W. Storti
* S. K. Upadhyaya

Foreword

* This presentation, prepared during my retirement, summarizes some of the engineering-based studies performed by the Plant Biomechanics Group at Cornell University.
* Chapters begin with puzzlements and end with conclusions.
* Some potential implications for climate-change studies are presented as "Conjectures."
* This content has been formatted as a bound book, a digital book and a video.
* Credit: The scanning electron micrograph image on the cover came from Troughton, John and Lesley A. Donaldson. 1972. Probing Plant Structure. Chapman and Hall, London.

Preface

This lecture is based upon StomateTutor 2.0 (J.R. Cooke, S.K. Upadhyaya, M.J. Delwiche, R.H. Rand, N.S. Scott, E.T. Sobel) which was a novel, computer-based presentation. It made extensive use of images within a HyperCard framework and provided pathways for multiple levels of users. It also included two Pascal programs, providing numerical simulation experiments using visual inputs.

This lecture is based upon the open-access publications at https://ecommons.cornell.edu/handle/1813/45423

JRC

StomateTutor was honored in 1991 with the
"Excellence in Teaching Materials Award"
by the Biological and Agricultural Engineering Division
of the American Society for Engineering Education.

Contents

Personal Background

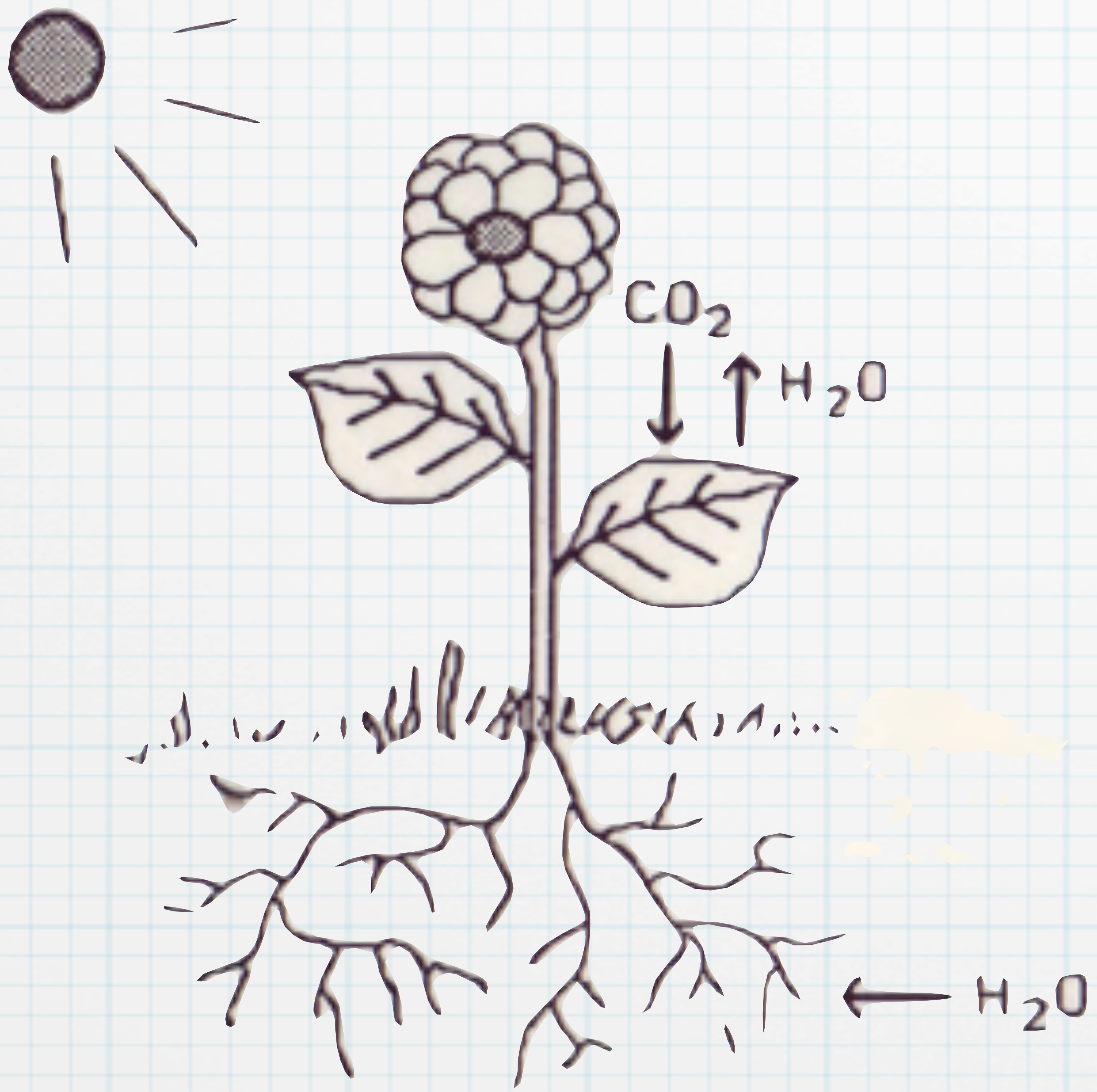
* Reared on a farm in northern Mecklenburg County, North Carolina
* Attended North Mecklenburg High and North Carolina State University
* Multidisciplinary Research – Engineering and Plant Biology
* Entire professional career was at Cornell University

General Comments

* Biological organisms are governed by the laws of physics and chemistry. (Techniques developed in the physical sciences may be transferred.)
* This is a multidisciplinary problem. (Biological Engineering, Chemistry, Physics, Information Technology, Engineering, etc.)
* In plant biology, complexities of geometry and non-homogeneous, non-isotropic materials are common.

*Reverse engineering

Ordinarily an engineering analysis pertains to a proposed, new design. In this case, however, the stomatal system already exists and is known to function successfully. Our task is to discover how it works, and perhaps to find ways to adapt it. By studying "successful" evolutionary designs, sometimes we can utilize the findings in contemporary engineering designs.

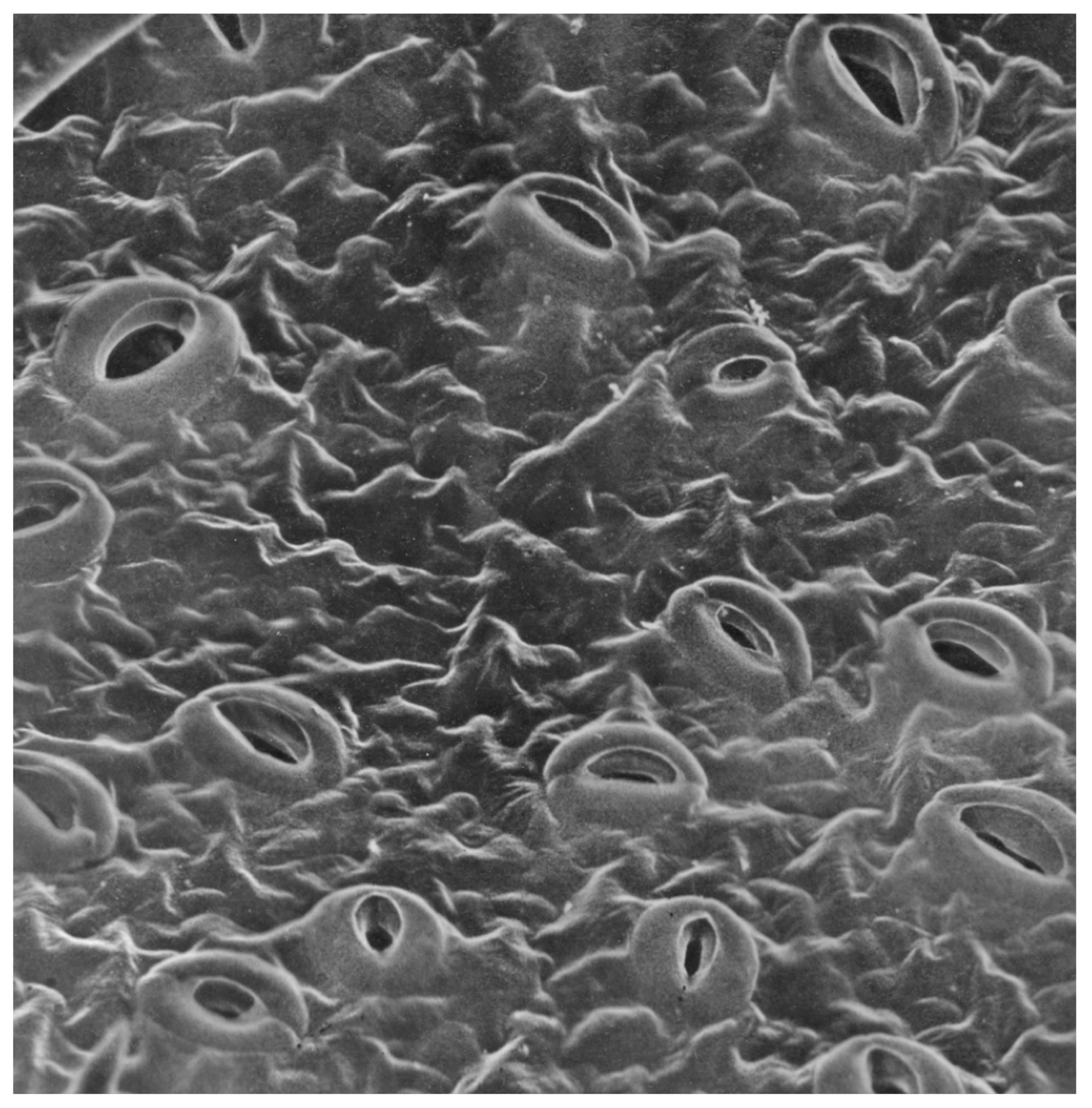


Biological Background

The photosynthetic process occurs largely in the leaf in the presence of light, and uses carbon dioxide from the air and water from the soil to form sugars and oxygen.

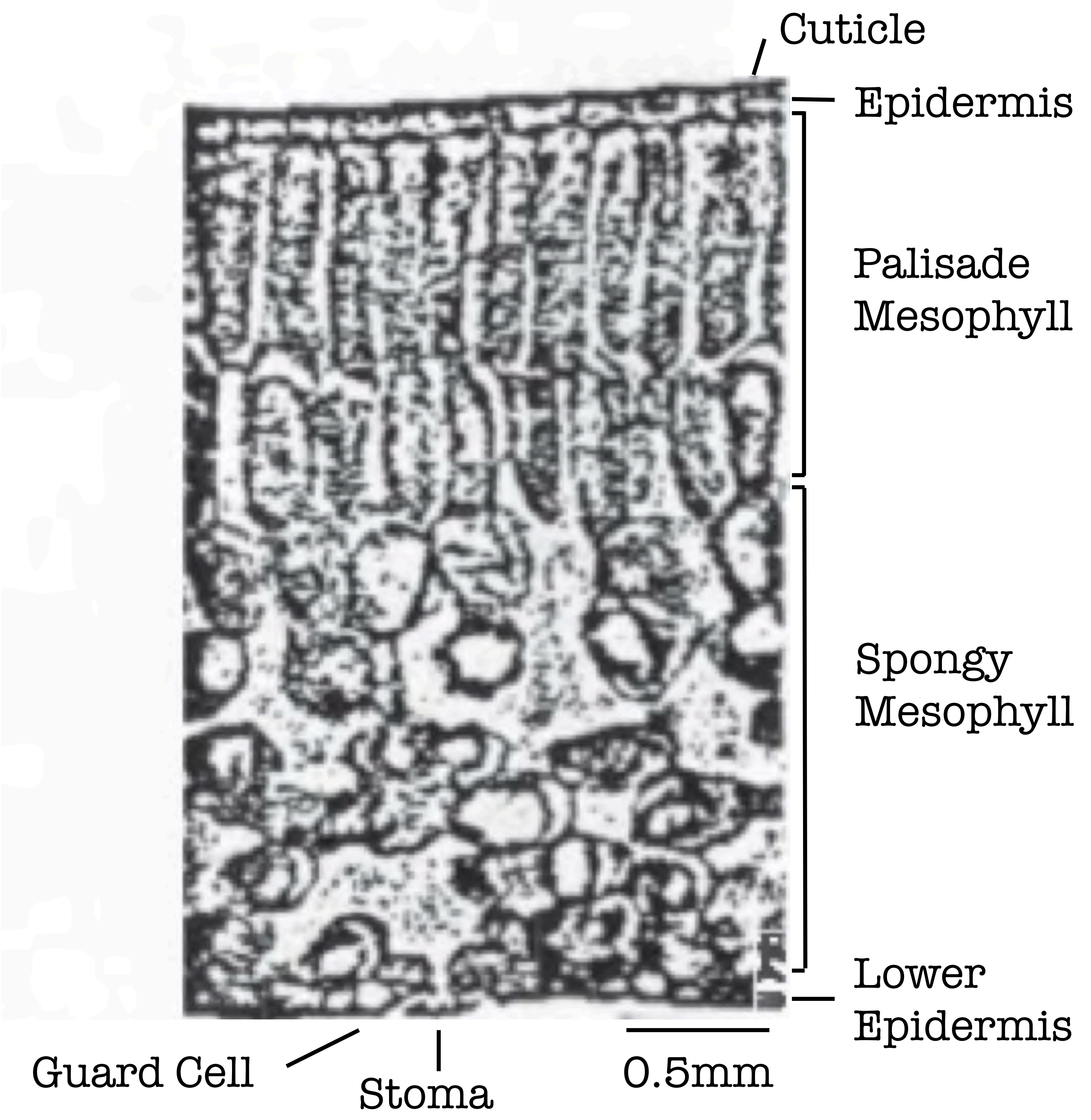
Stomata
(scanning electron micrograph of cucumber leaf)

* Stomata are the regulating valves on the surface of higher plants that control gaseous exchanges (water, oxygen and carbon dioxide) between plants and their environments.



Troughton, John and Lesley A. Donaldson. 1972. Probing Plant Structure. Chapman and Hall, London.

Stomatal Control of Diffusion



Adapted from Keeton and Gould, 4th edition. p 274, 1986

Leaf Cross-section

* Cuticle on the surface **impedes exchange of gases** with the environment (and helps avoid desiccation).
* Stomata **(size-varying microscopic pores)** control gas exchanges between the plant and its environment.
* Stomata **mediate competing processes** – allowing carbon dioxide entry – but limiting water loss. (This diffusion is through shared stomatal pores, but in opposite directions!)

General

* A vast stomatal literature (for more than 1.6 centuries, e.g., von Mohl, 1856) contains many core puzzlements.
* This research was motivated by puzzlements about stomata.
* Strategy: Subdivide into parts, analyze, and then recompose.

Stomatal Diffusion

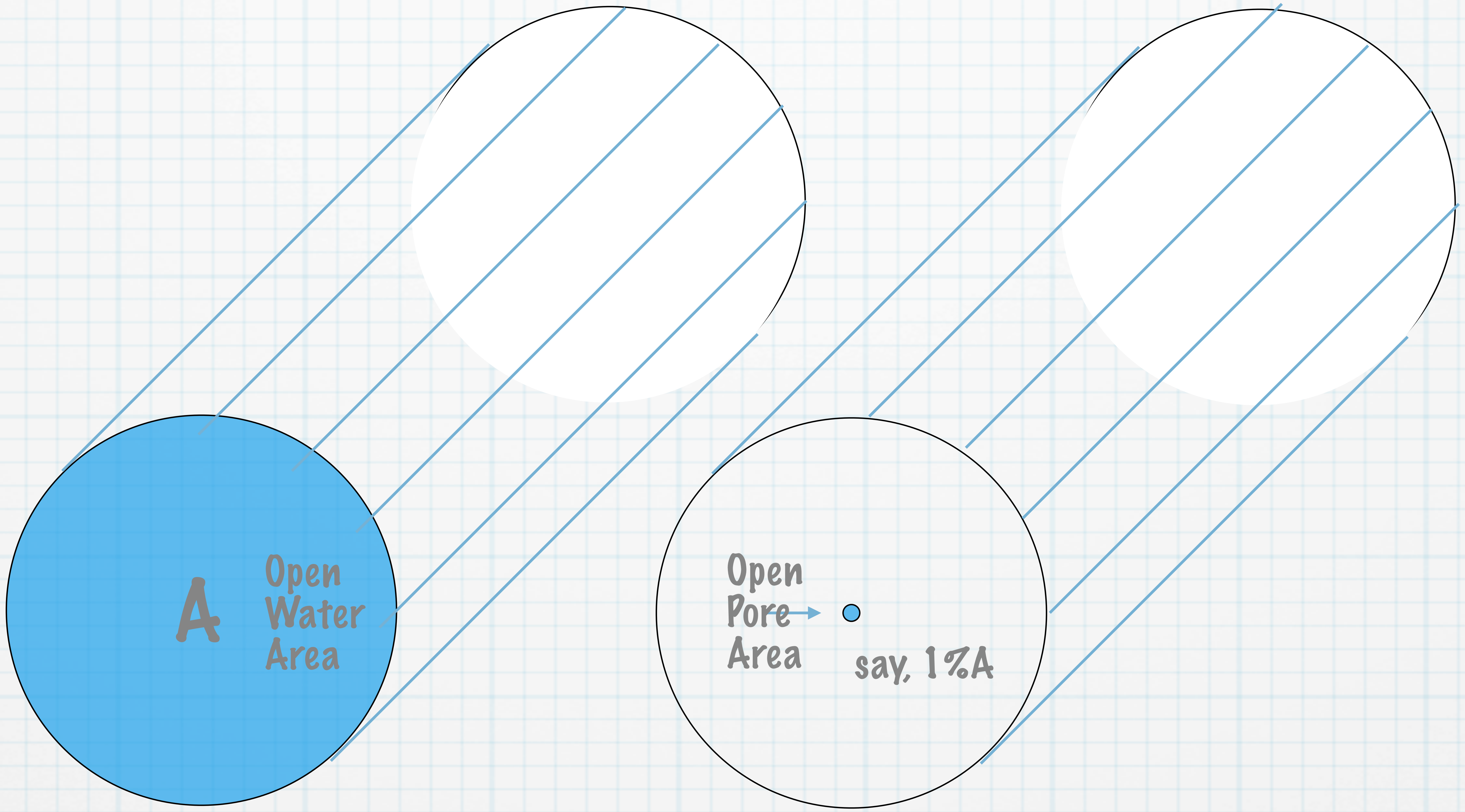
Part 1

Puzzlements - 1

(diffusion)

Although open stomatal pores may account for perhaps only **one percent** of the stomate bearing surface, the rate of stomatal water loss per unit leaf area may be **more than half the rate of evaporation from an exposed water surface of the same area.**

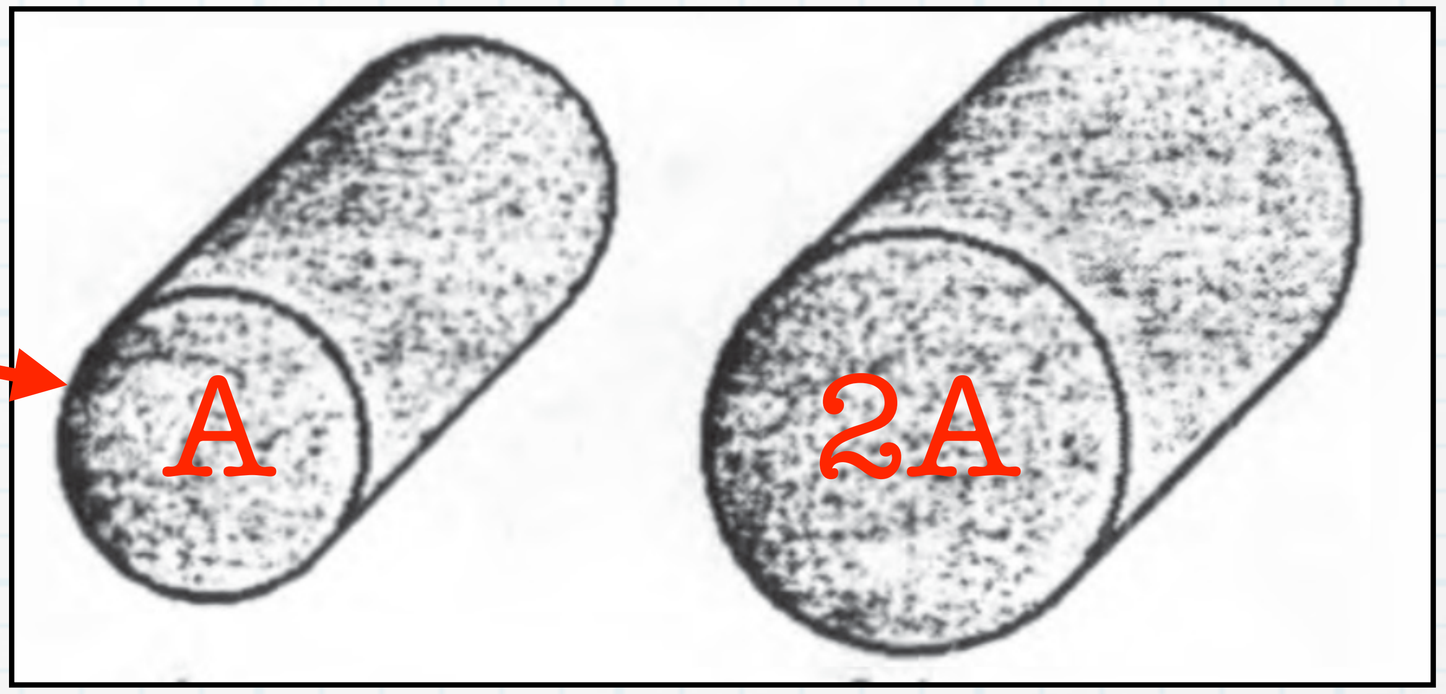
- How can this happen with such a small fraction of the leaf's interior exposed?
- How significantly does stomatal spacing affect diffusion rate?
- How can control of stomatal diffusion be achieved with such small changes in pore width?



If an open water area at the end of a cylinder is reduced to 1%, what would be the diffusion rate?

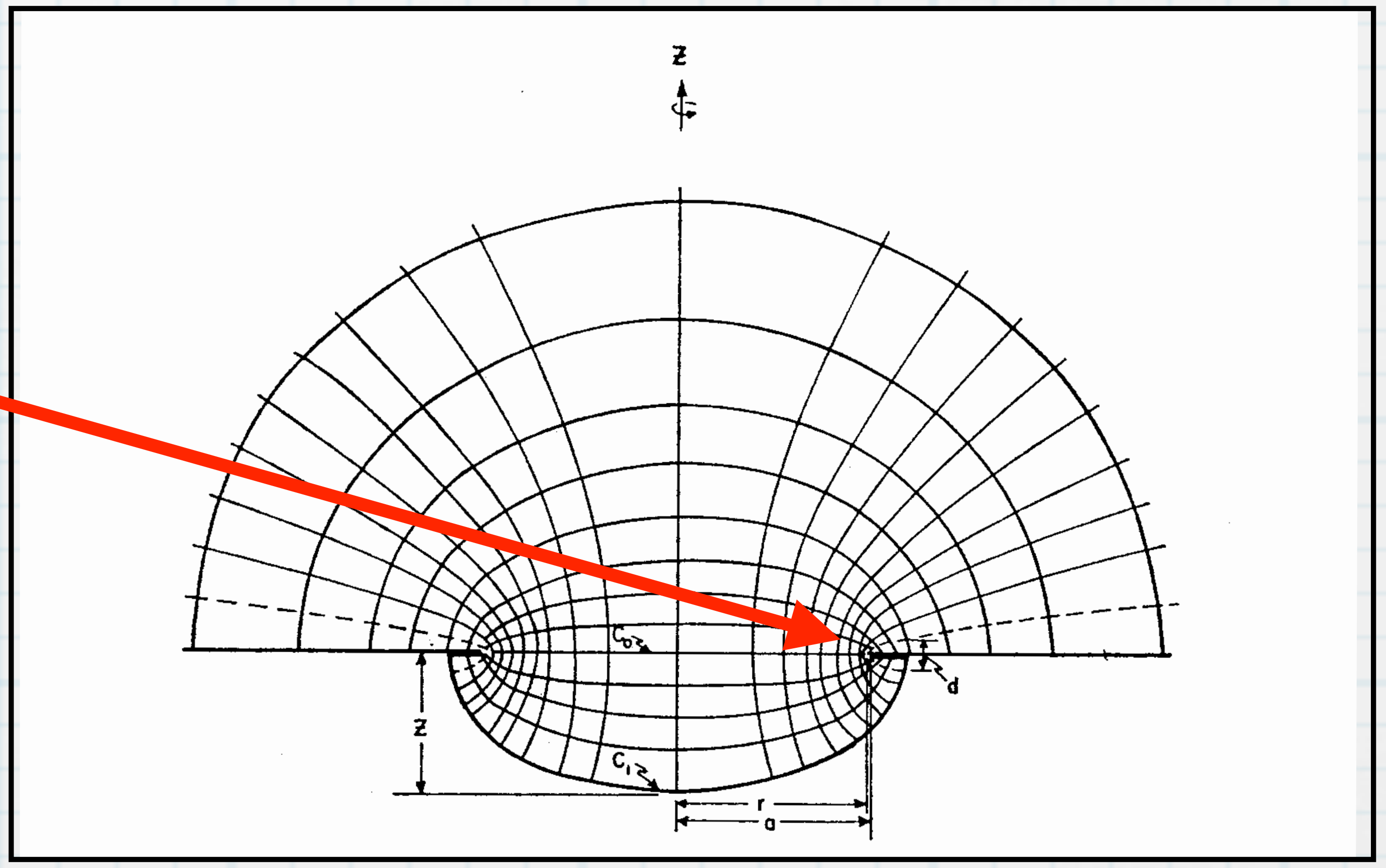
Diffusion rate is proportional to <u>local</u> concentration gradient

* For straight-line diffusion, the rate is proportional to cross-sectional area.

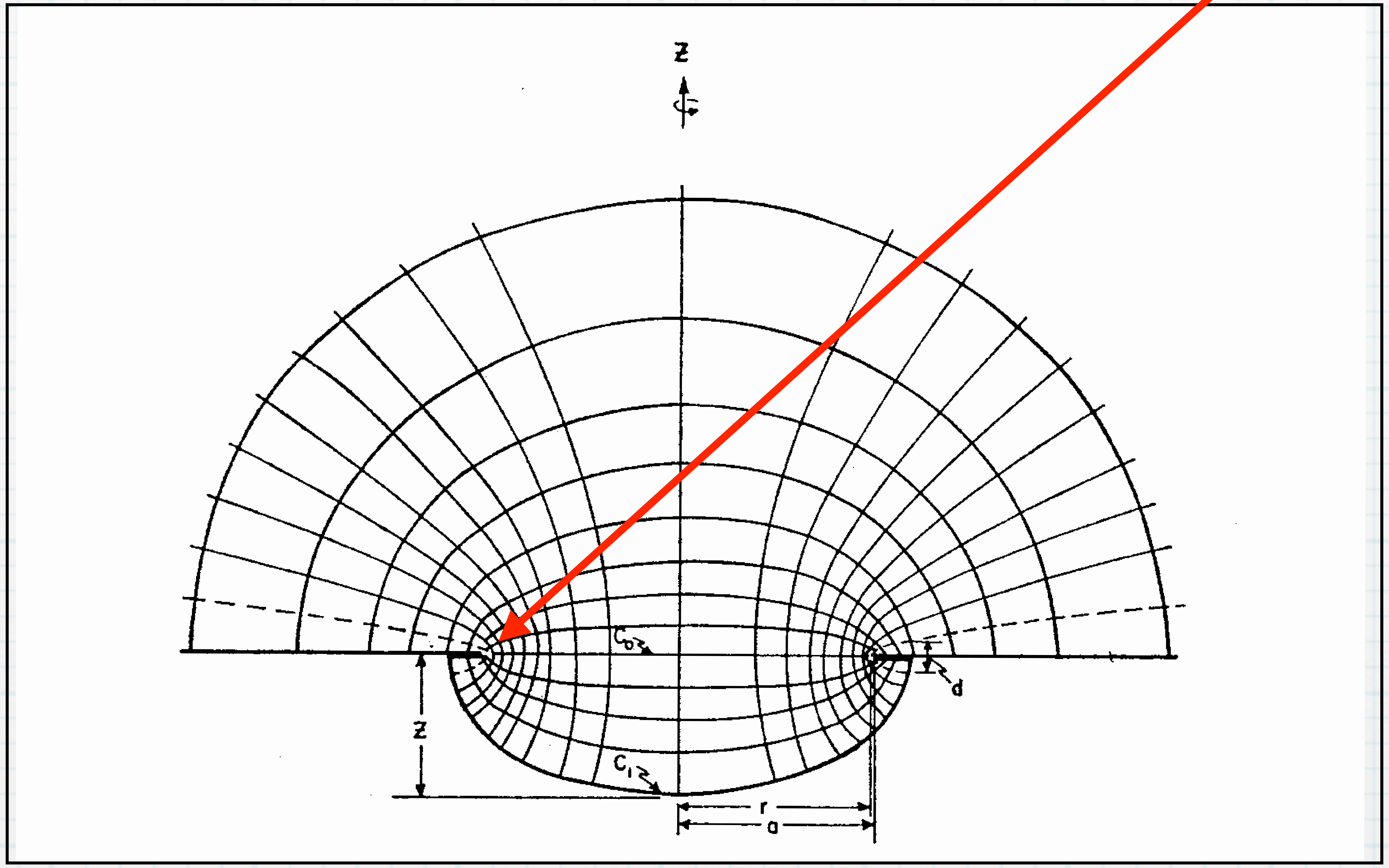


(doubling area doubles diffusion)

* Curved diffusion lines at the edge of a pore increase the local concentration gradient – therefore, the local diffusion rate at the pore's edge is increased.



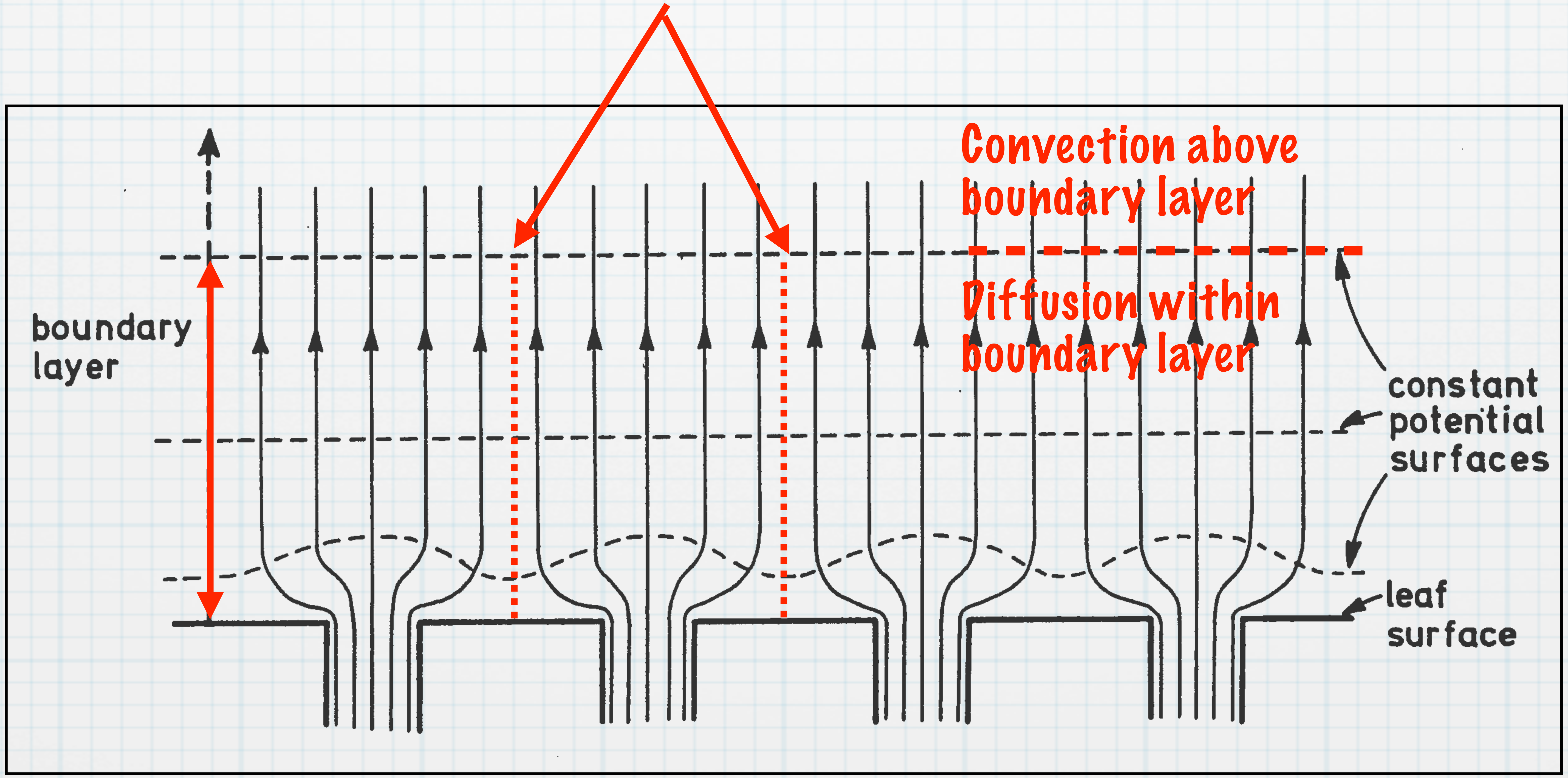
The constant concentration lines (surfaces) at a pore become more closely spaced at the edges – increasing the **local** concentration gradient there.



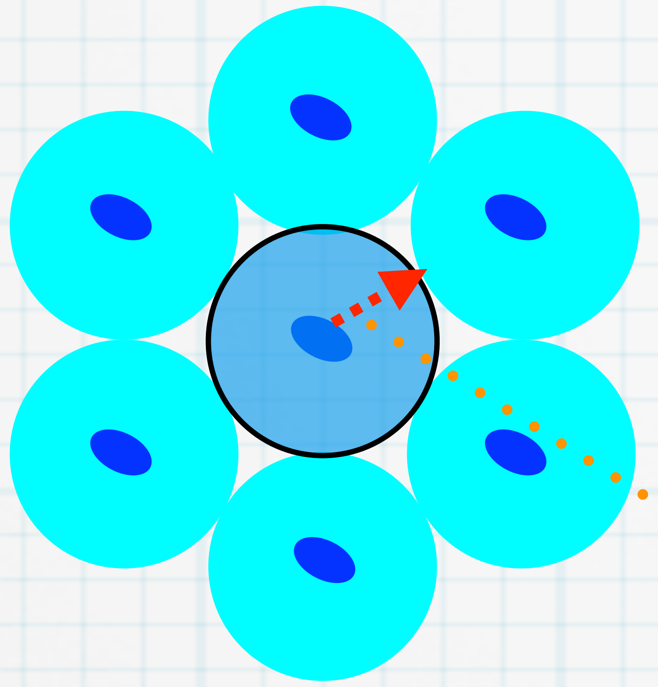
[For an isolated, circular pore, the constant concentration surfaces are oblate spheroids, i.e., door knob-shaped.]

Diffusion occurs through a boundary layer adjacent to the leaf.

* A boundary layer occurs at the leaf surface.
* Diffusion is bounded horizontally by adjacent pores
* Transport above the boundary layer is by convection
* Formulate as a three-dimensional boundary value problem



3-D Model

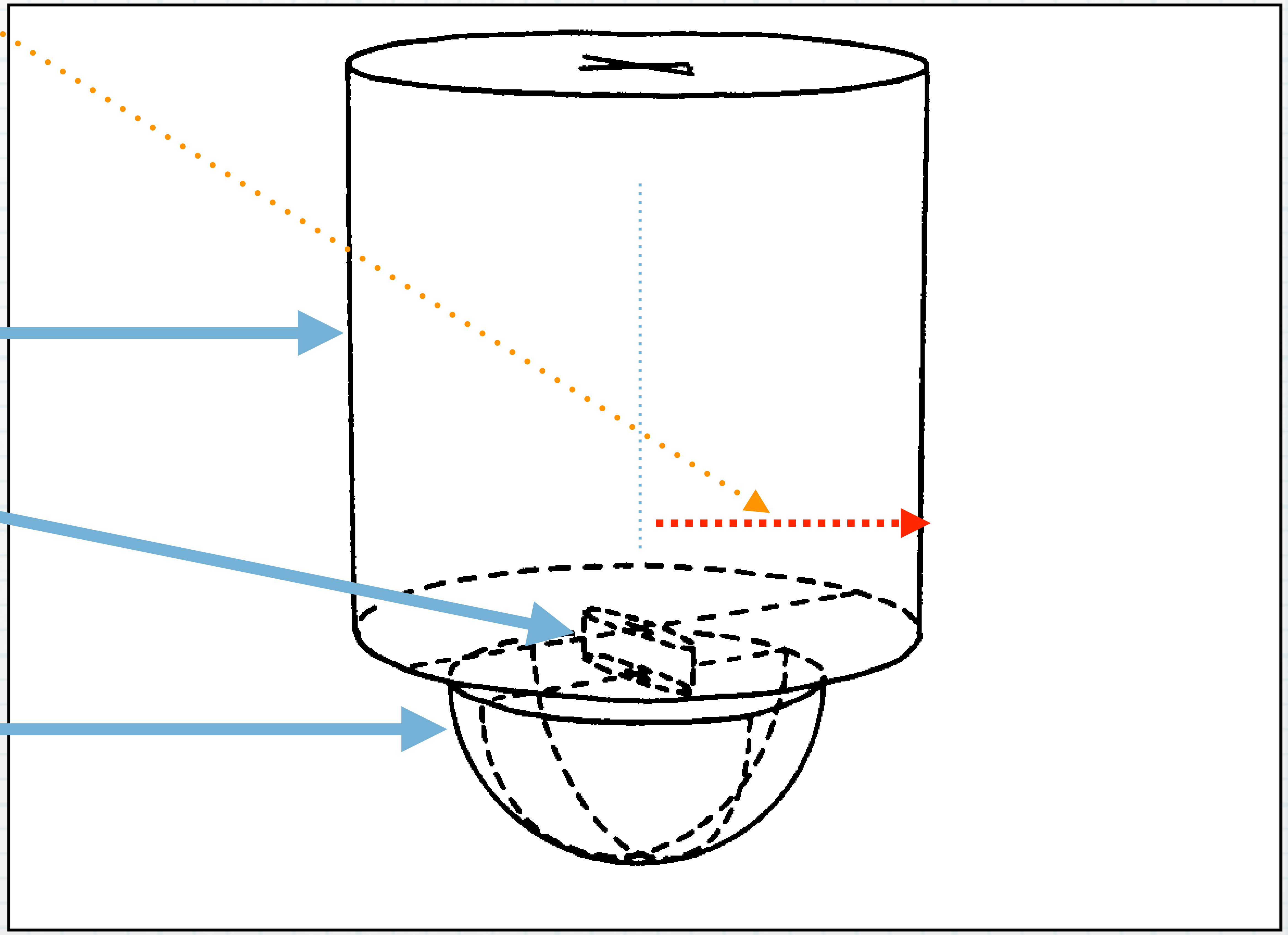


If we assume a circular array of stomata (at left), there will be no radial exchange among the pores.

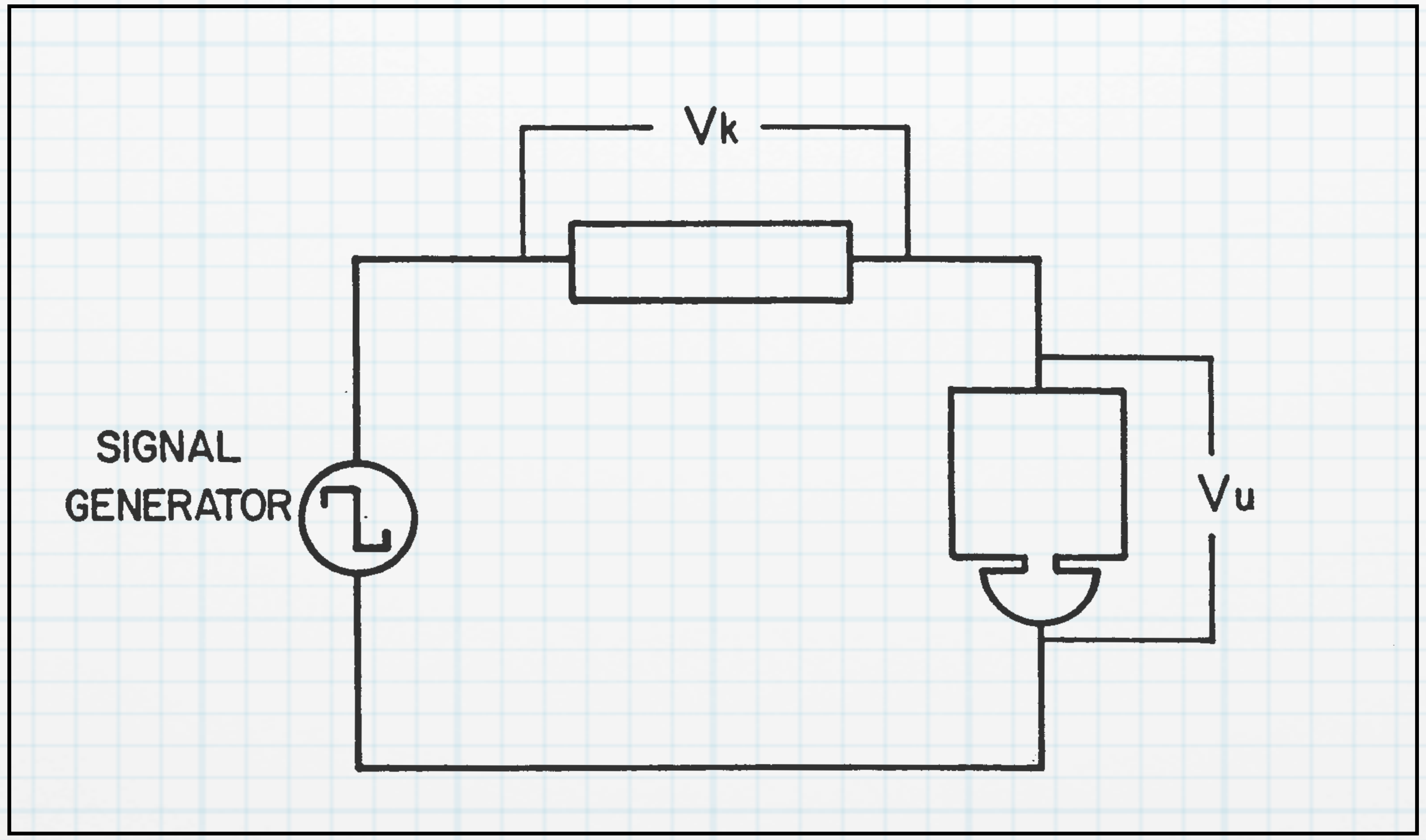
Boundary layer

Elliptical pore

Hemispherical substomatal cavity



Physical Analog for Stomatal Diffusion



* An electrolytic tank analog is governed by the same equation.

Holcomb, D.P., and J.R. Cooke. 1977. An electrolytic tank analog determination of stomatal diffusion resistance. ASAE Paper No. 77-5510. 50 pages.

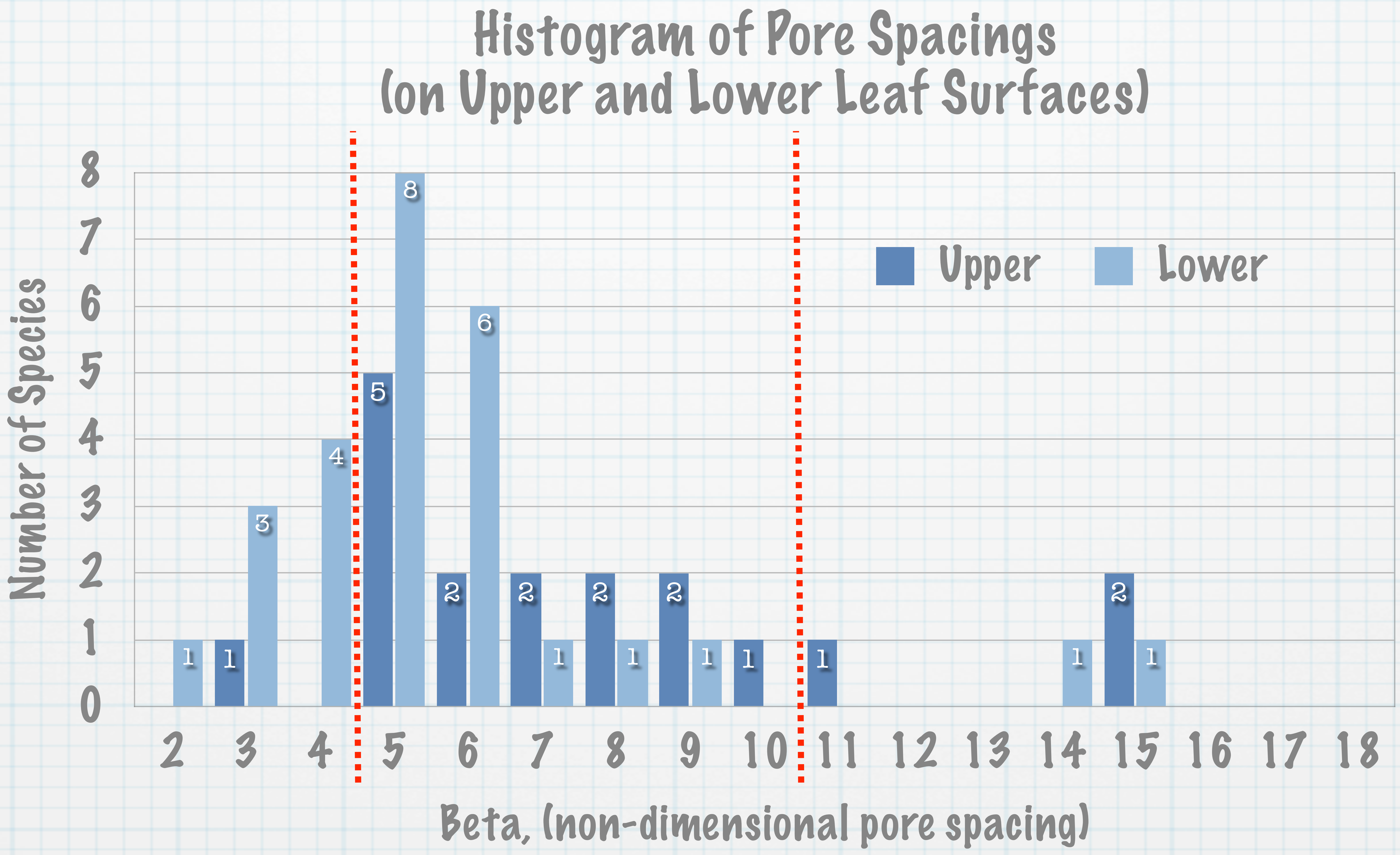
https://ecommons.cornell.edu/handle/1813/45423

Non-Dimensional Variables

The following graphs use Non-Dimensional Variables
[scaled to the pore's (constant) semi-length]

- **Pore width, alpha**
  ratio of pore width to pore length, (0.05 <= alpha <=0.5) [often 0.2 or less]
- **Pore spacing, beta**
  ratio of the pore spacing cylinder radius
  to the elliptical pore's semi-length, (beta >= 2.0) [often 5 to 10]
- **Boundary layer thickness, T**
  ratio of the pore spacing cylinder length
  to the ellipse semi-length, (T >= radius of the pore spacing cylinder),
  [approx. 25 to 250 times half the pore length; wind speed dependent]
- **Fractional area of open pores**
  (alpha/beta squared) [approx. 0.005 to 0.020 i.e., approx 0.5% to 2.0%]

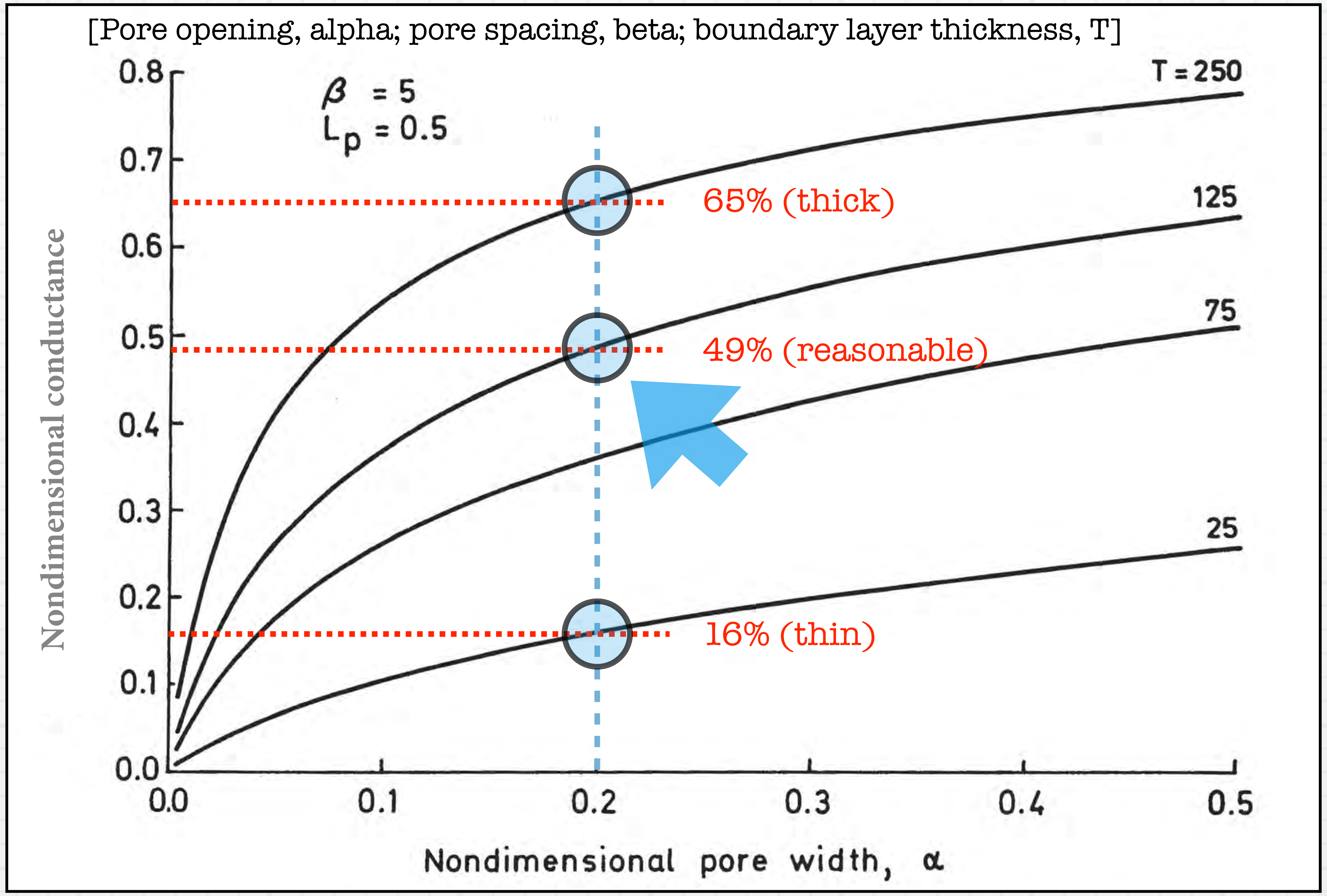
Pore spacing for a variety of species



Data taken from Meidner, H. and T. A. Mansfield. 1968. Physiology of Stomata, McGraw-Hill.

Pore spacings (beta) of 5 to 10 are common.

Diffusion rate vs pore width & boundary layer thickness

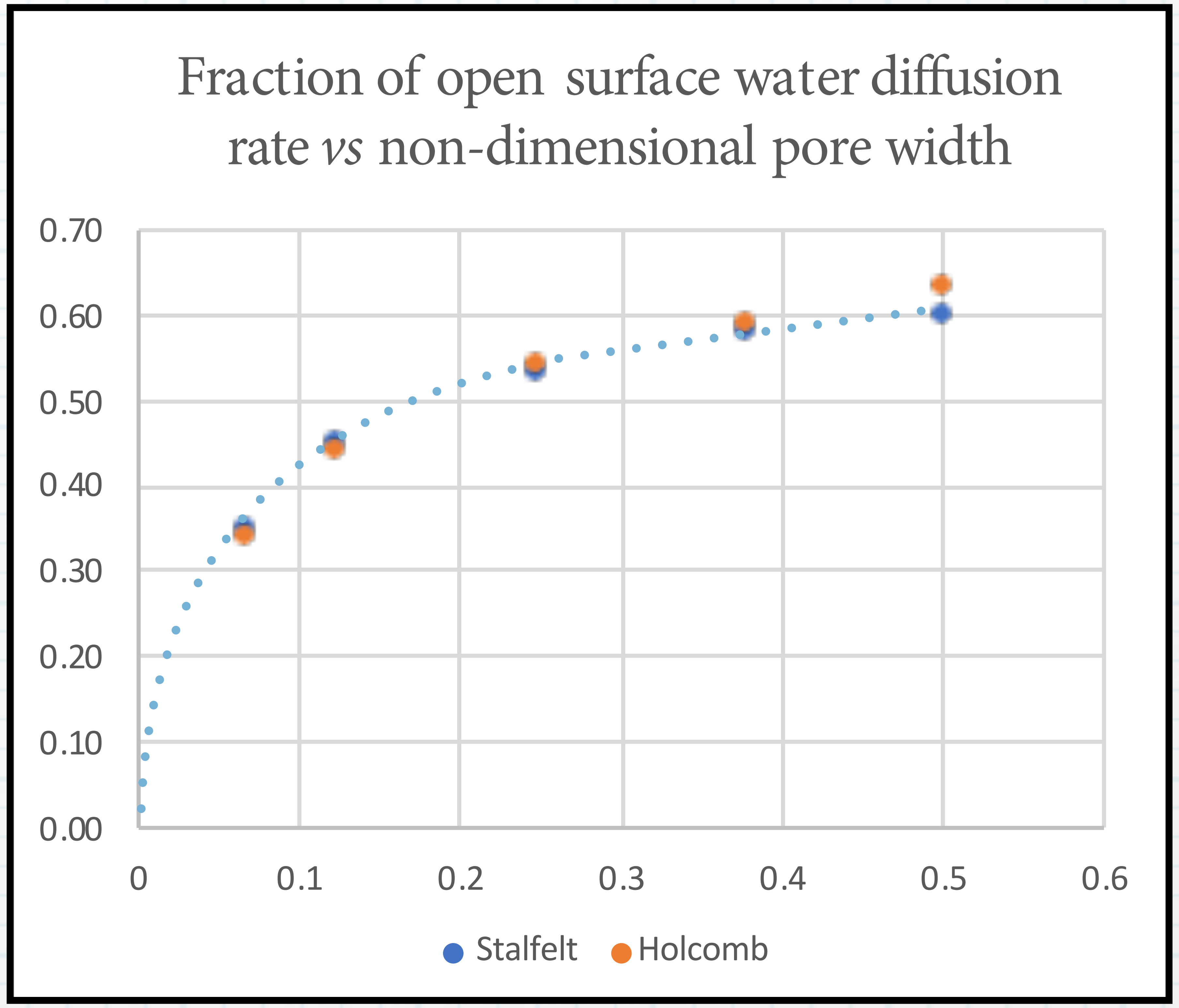


For a pore spacing (5), pore width (0.2), and reasonable boundary layer thickness (125), the diffusion rate can be HALF that of a free surface of water of the same size!

Comparison of experimental and predicted stomatal water loss

Stoma Width, alpha	Stalfelt (exper. fraction)	Holcomb (predicted fraction)
0.068	0.35	0.34
0.125	0.45	0.44
0.250	0.53	0.54
0.380	0.58	0.59
0.500	0.60	0.63

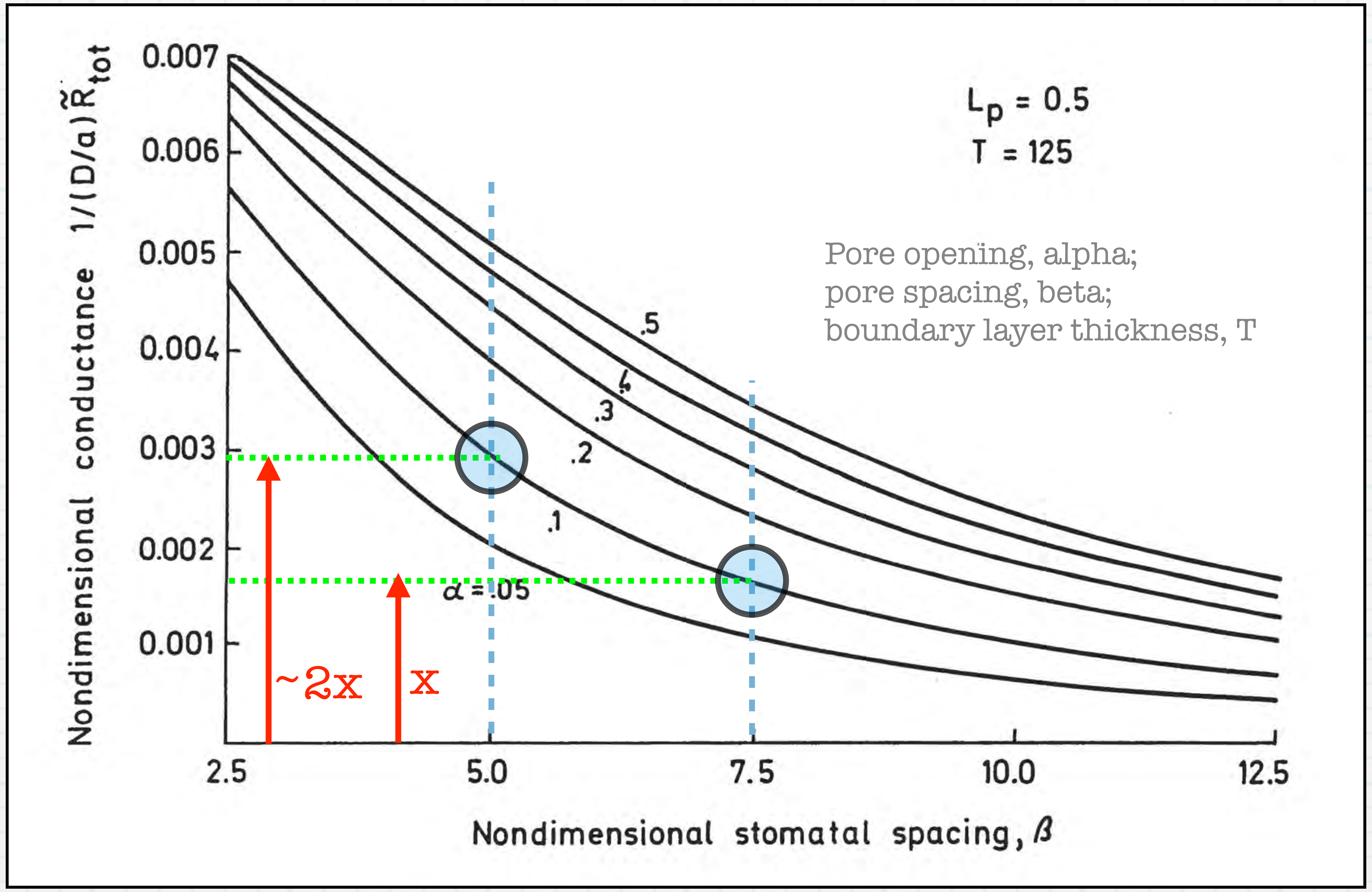
Stomatal Water Diffusion Rate as a Fraction of Open Surface Water Diffusion Rate



Holcomb, D.P., and J.R. Cooke. 1977. An electrolytic tank analog determination of stomatal diffusion resistance. ASAE Paper No. 77-5510. 50 pages.

This is a surprisingly large diffusion rate with a small open pore area. Note the agreement of experimental and predicted!

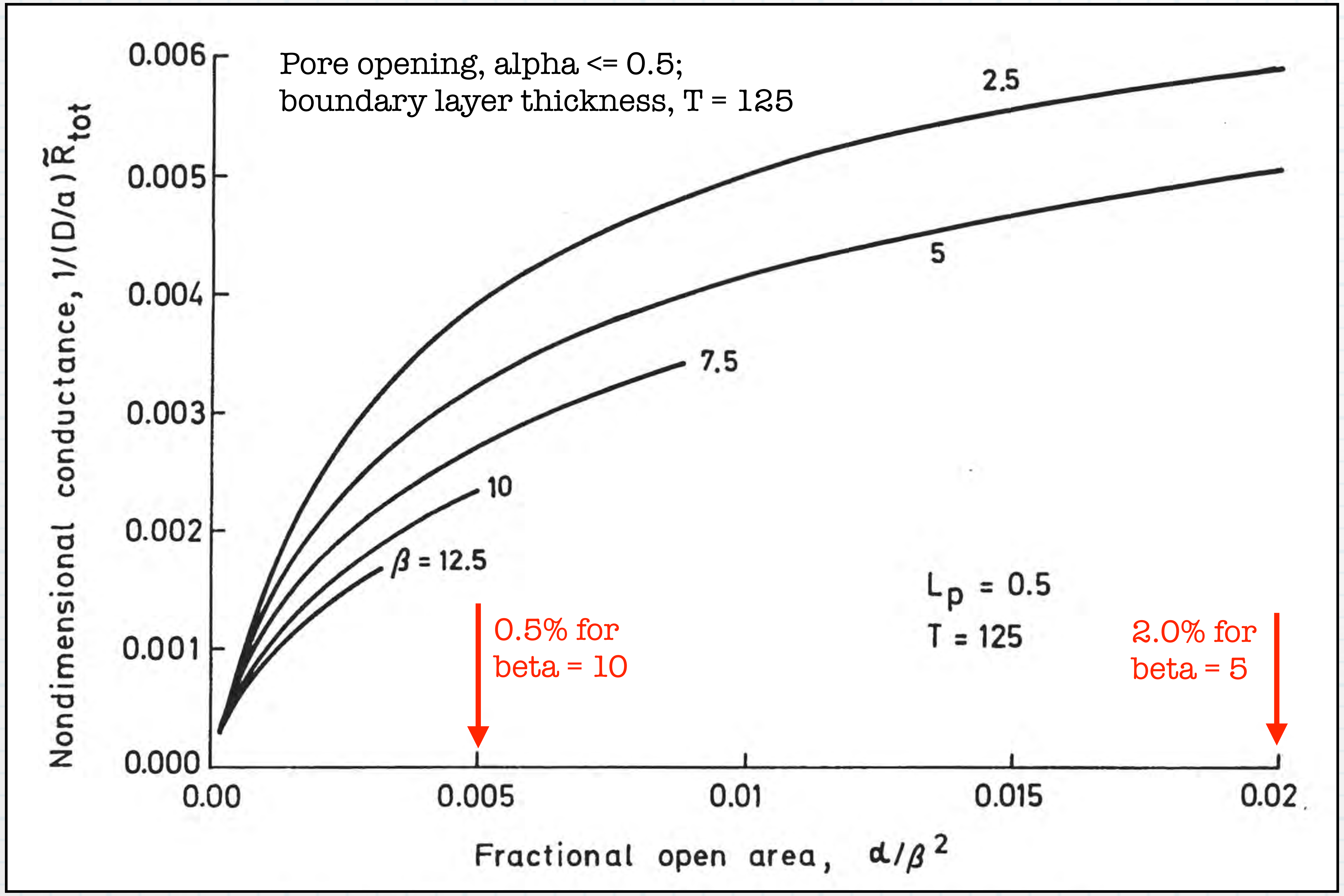
Diffusion rate vs stomatal spacing



Diffusion rate doubles if pore spacing is reduced from 7.5 to 5.0 (for pore opening 0.1)

Diffusion rate vs fractional open area

for several values of pore spacing



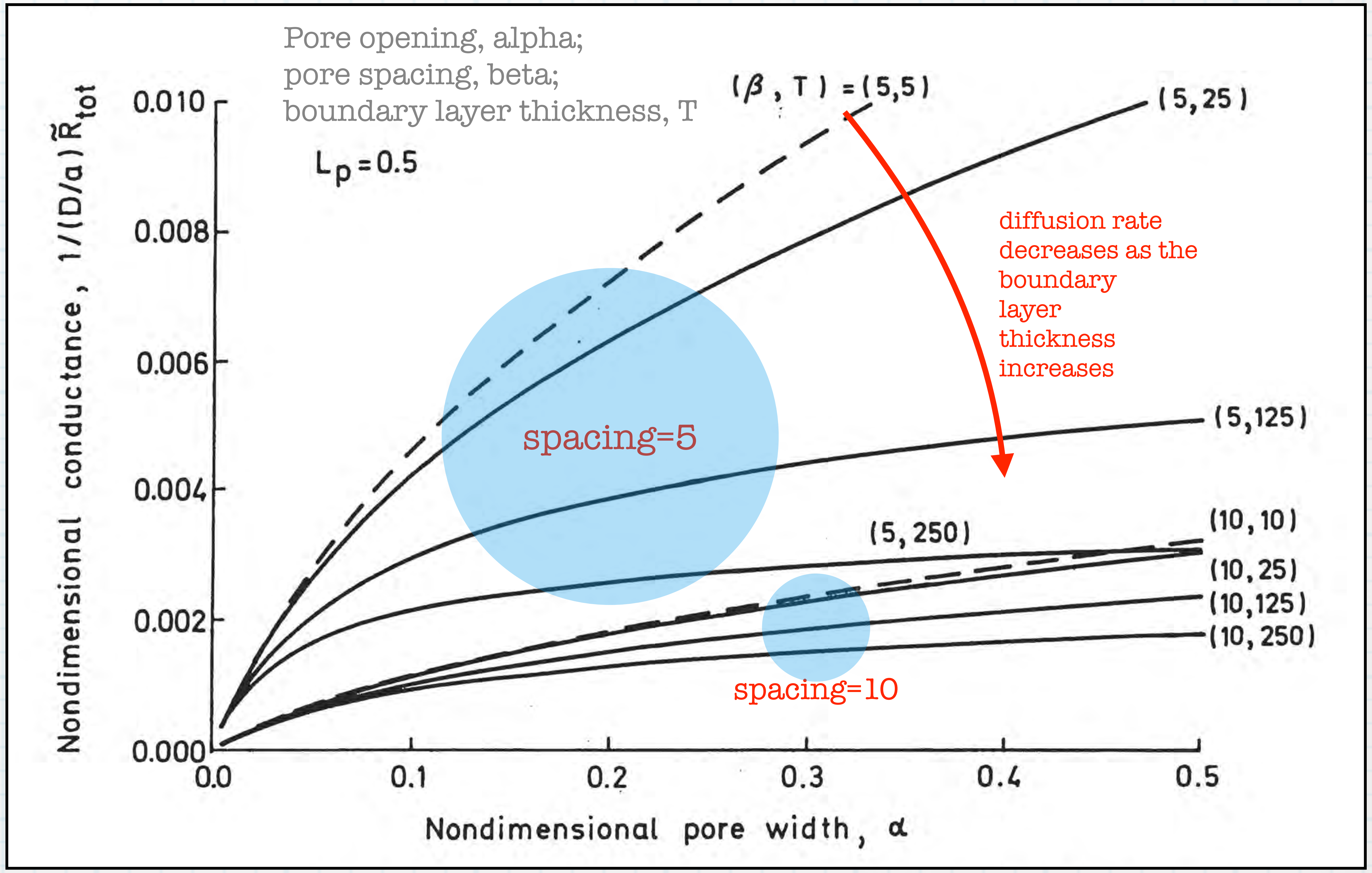
- For pore widths <= 0.5, the fractional area of the open pores is small –
  - <= 0.5% for pore spacing = 10
  - <= 2.0% for pore spacing = 5
- Diffusion is NOT proportional to the fractional open pore area.

Diffusion rate vs pore width

for several values of

pore spacing & boundary layer thickness

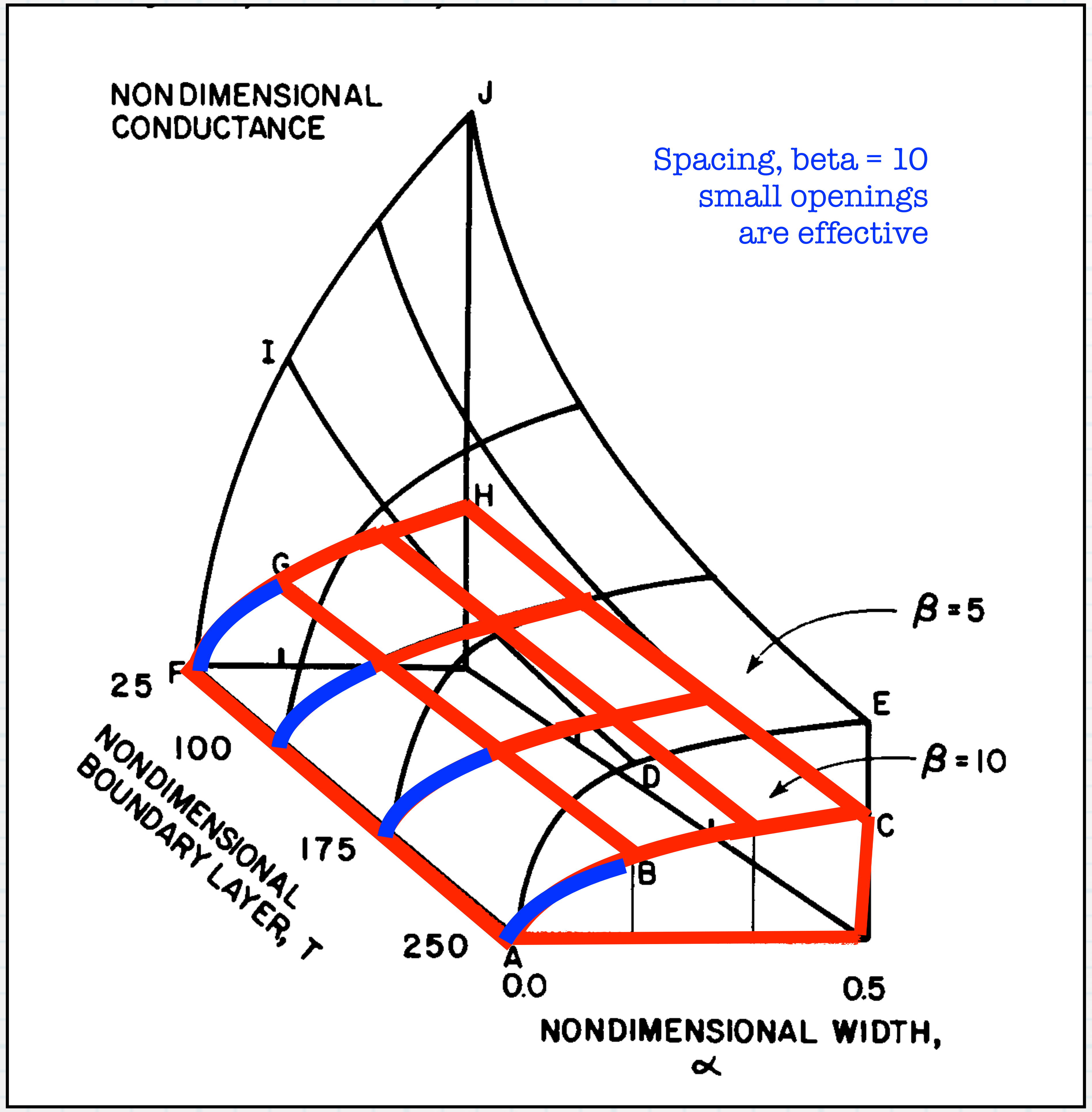
- The diffusion rate per unit leaf area is substantially higher for a closer pore spacing (beta=5) than for a wider pore spacing (beta =10).

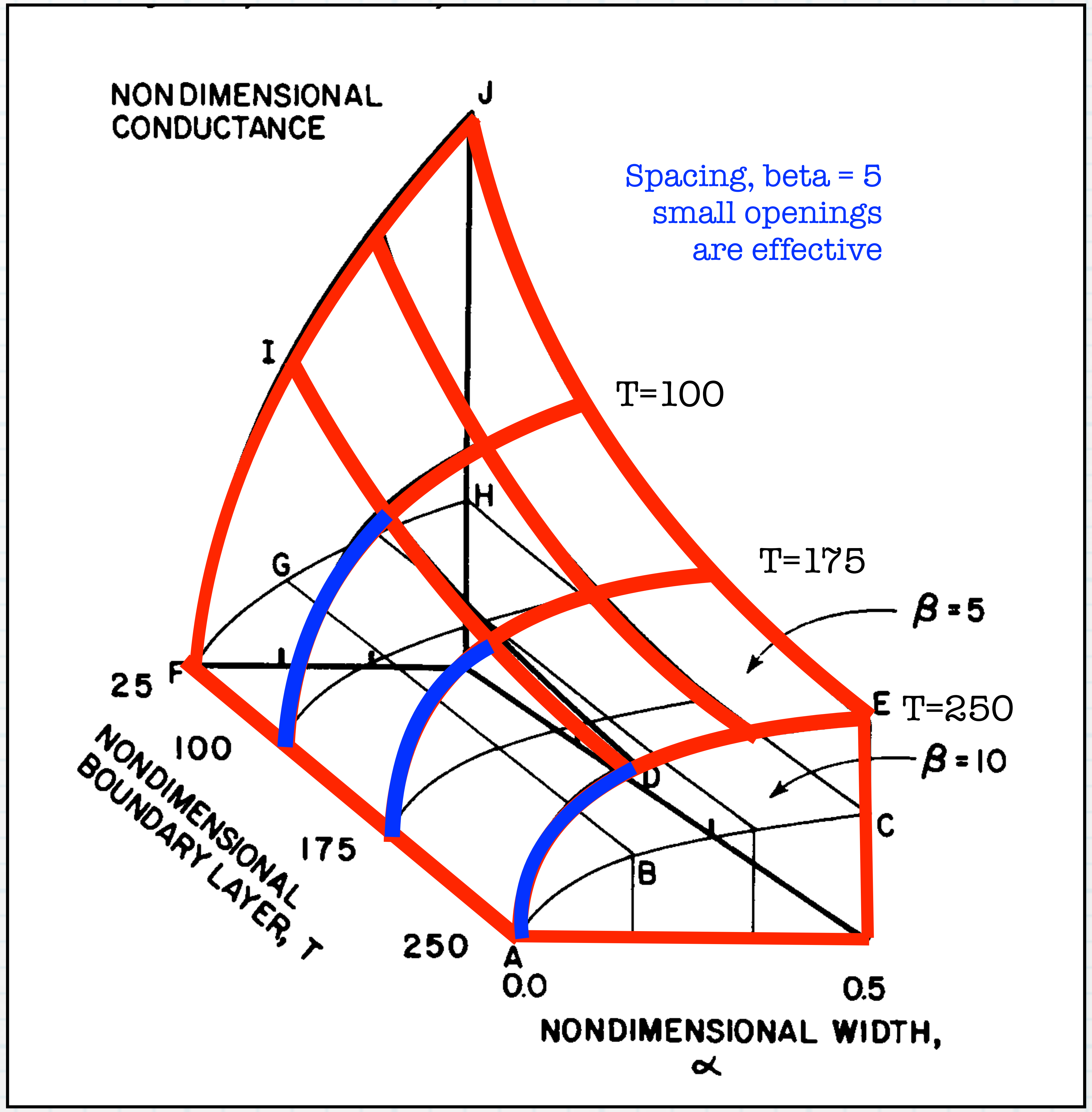


- The diffusion rate decreases as the boundary layer thickness increases, especially for closer pore spacing.

- The dashed lines show diffusion rate for isolated pores. This reveals the extent of 'mutual interference' if isolated pores were simply superimposed.

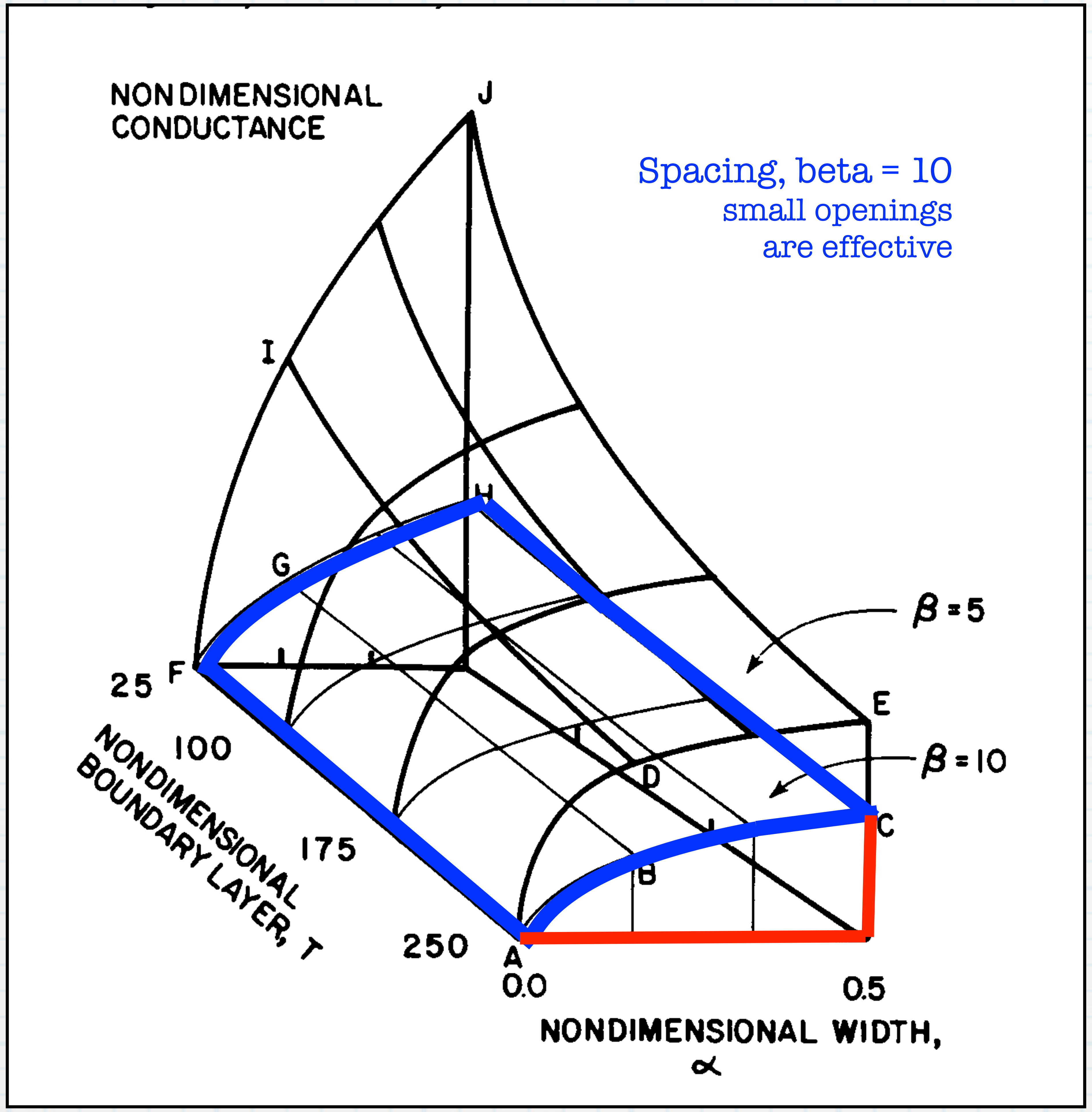
Diffusion rate vs pore width

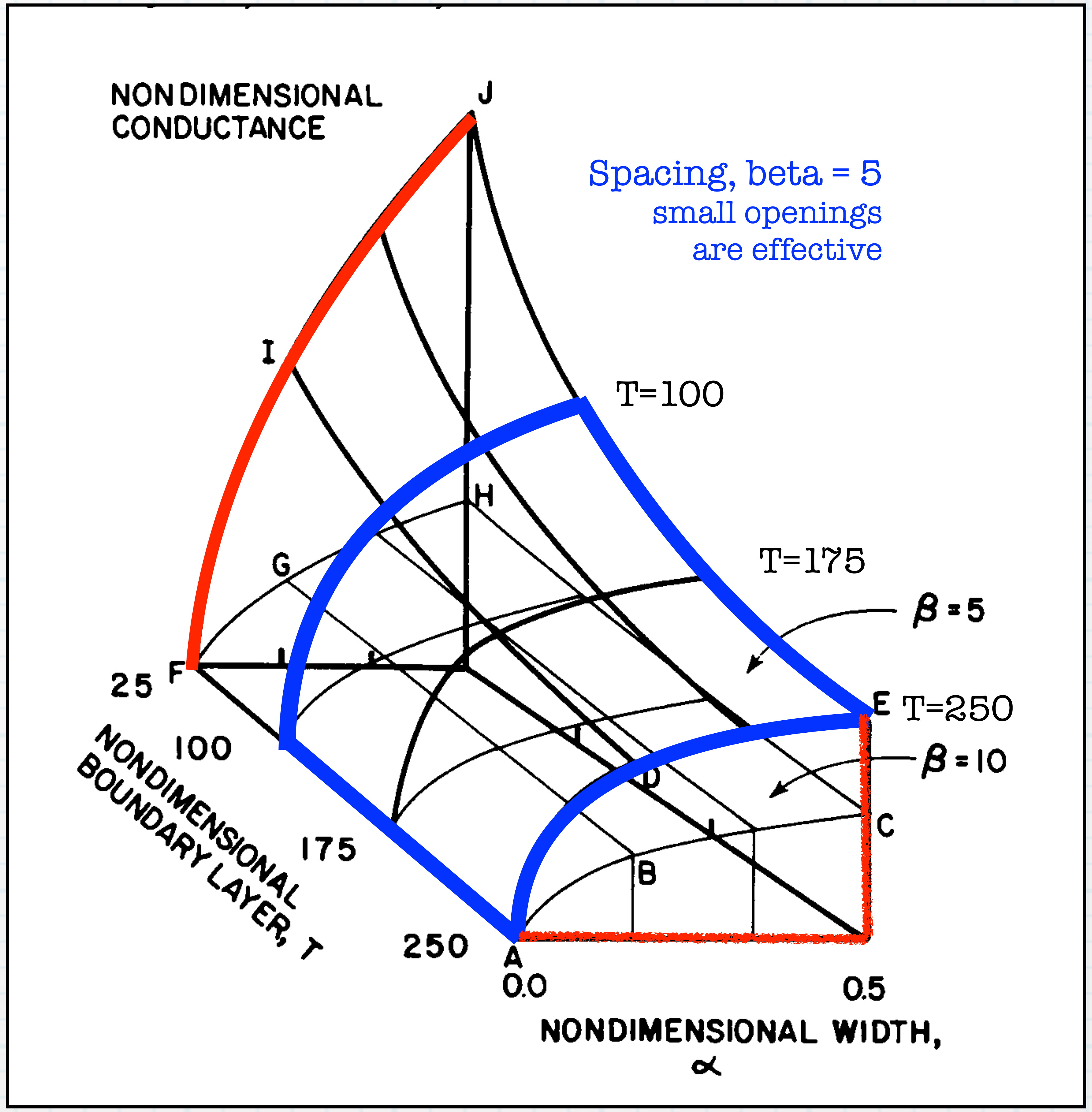




* Diffusion rate increases sharply when the pore initially opens (small alpha), but increases less sharply for wider pores. [Largely acts as an off/on valve.]

Diffusion rate vs boundary layer thickness





* Diffusion rate is relatively independent of wind speed, e.g., T >= 100, for typical pore spacings (beta of 5 to 10) !! [Note: T decreases with increasing wind speed.]

Conclusions

(stomatal diffusion-1)

* Stomatal diffusion rate increases sharply as the pore begins to open, but increases less sharply as the pore widens (>0.2), except for very thin boundary layers or dense stomatal spacings. [Diffusive control can be achieved with small changes in pore widths, making larger widths unnecessary (which would require more ATP energy).]

* There exists <u>no</u> geometry at which diffusion per unit stomate-bearing surface achieves a <u>relative</u> maximum, but increases monotonically with increasing pore width and with decreasing pore spacing and boundary layer thickness. [Diffusion rate depends not just on pore anatomy, but significantly upon <u>both</u> pore spacing and boundary layer thickness.]

Conclusions

(stomatal diffusion-2)

* Stomatal diffusion rate can become a large fraction of that from a free water surface. This depends upon pore geometry, BUT ALSO upon boundary layer thickness. [While exposing only a very small fraction of the leaf's interior, the stomatal diffusion rate can be a major fraction of the diffusion rate for open water.]
* For typical pore spacings, gas exchange rates are relatively insensitive to boundary layer thickness changes. [More closely spaced pores would increase diffusion rate, BUT would cause an undesirable dependence upon wind speed.]
* Diffusion rate is not simply proportional to the pore area or the pore perimeter.

Structural Mechanics of Guard Cell Pairs

Part 2

Review - 1
(diffusion)

In the previous chapter we considered the leaf, a natural solar collector, as the structure that provides an **environment for the photosynthetic process.**

The **cuticle limits gaseous exchanges** with the external environment - restricting desiccation and stabilizing the internal environment.

Gaseous exchanges occur through **microscopic, width-varying pores,** called **stomata.**

The leaf's design facilitates a **truly remarkable diffusive capacity.**

Review - 2

(diffusion)

The role of stomatal pore dimensions, stomatal density and boundary layer were examined in depth.

- Diffusive control requires **only small pore-width openings**, exposing perhaps only 1% of the leaf's surface area when fully open, **leaving most of the interior unexposed.**

- Diffusion rate depends **not just on pore anatomy**, but significantly also upon **both pore spacing and boundary layer thickness.**

- Diffusion rate **increases with increased stomatal density**, but **an undesirable dependence upon wind speed would result for densities higher than commonly occur.**

Let's now consider the structural features of stomata that enable the pore to open and close.

Puzzlement - 2
(structural mechanics)

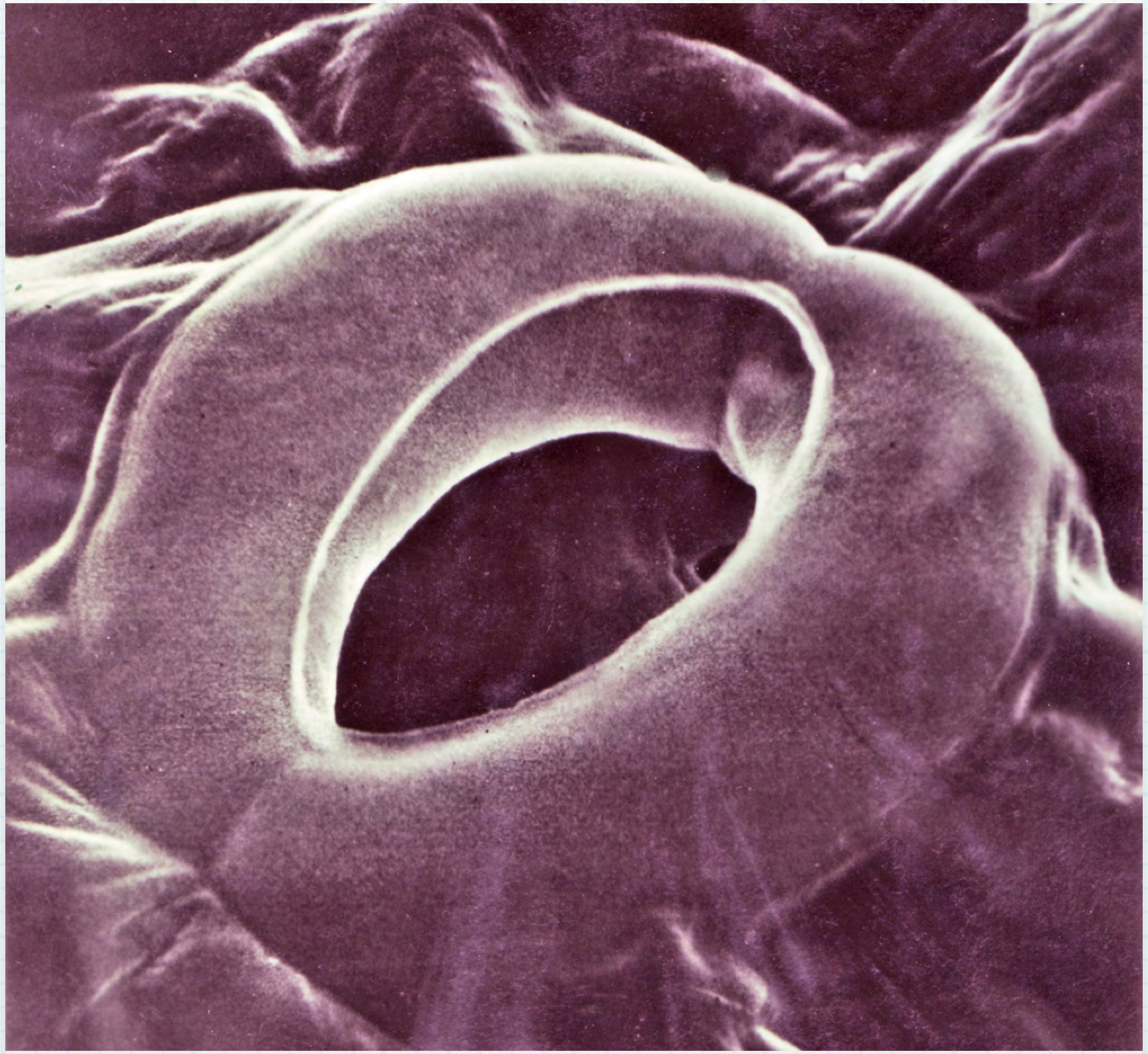
During daytime (with sunshine), the pore should be open if sufficient water is available; but if a water deficit occurs, it should close.

During nighttime, the pore should be closed to avoid water loss.

What structural features allow the stomatal pore to open and close?

A closer view (cucumber)

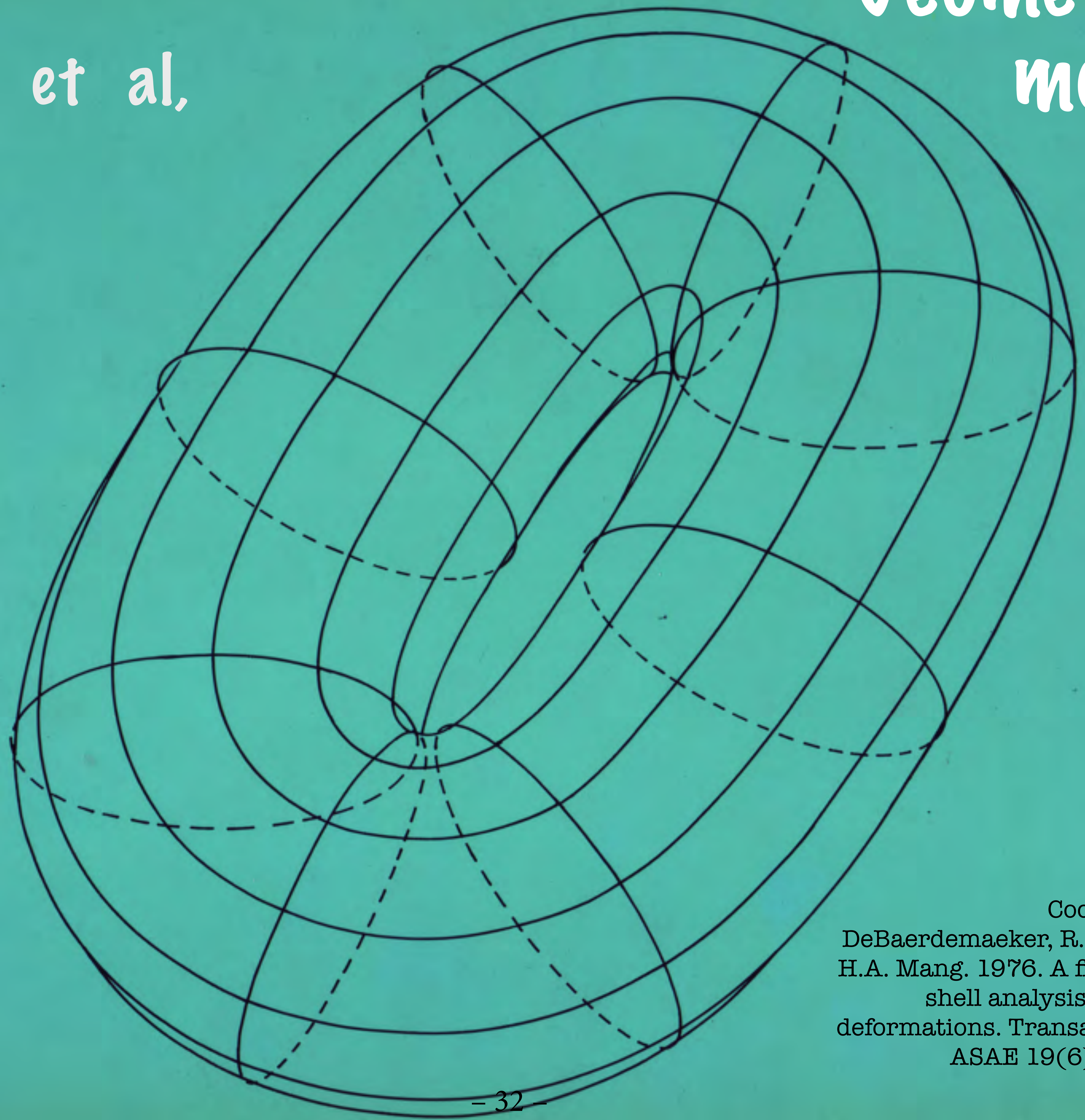
(Troughton and Donaldson)



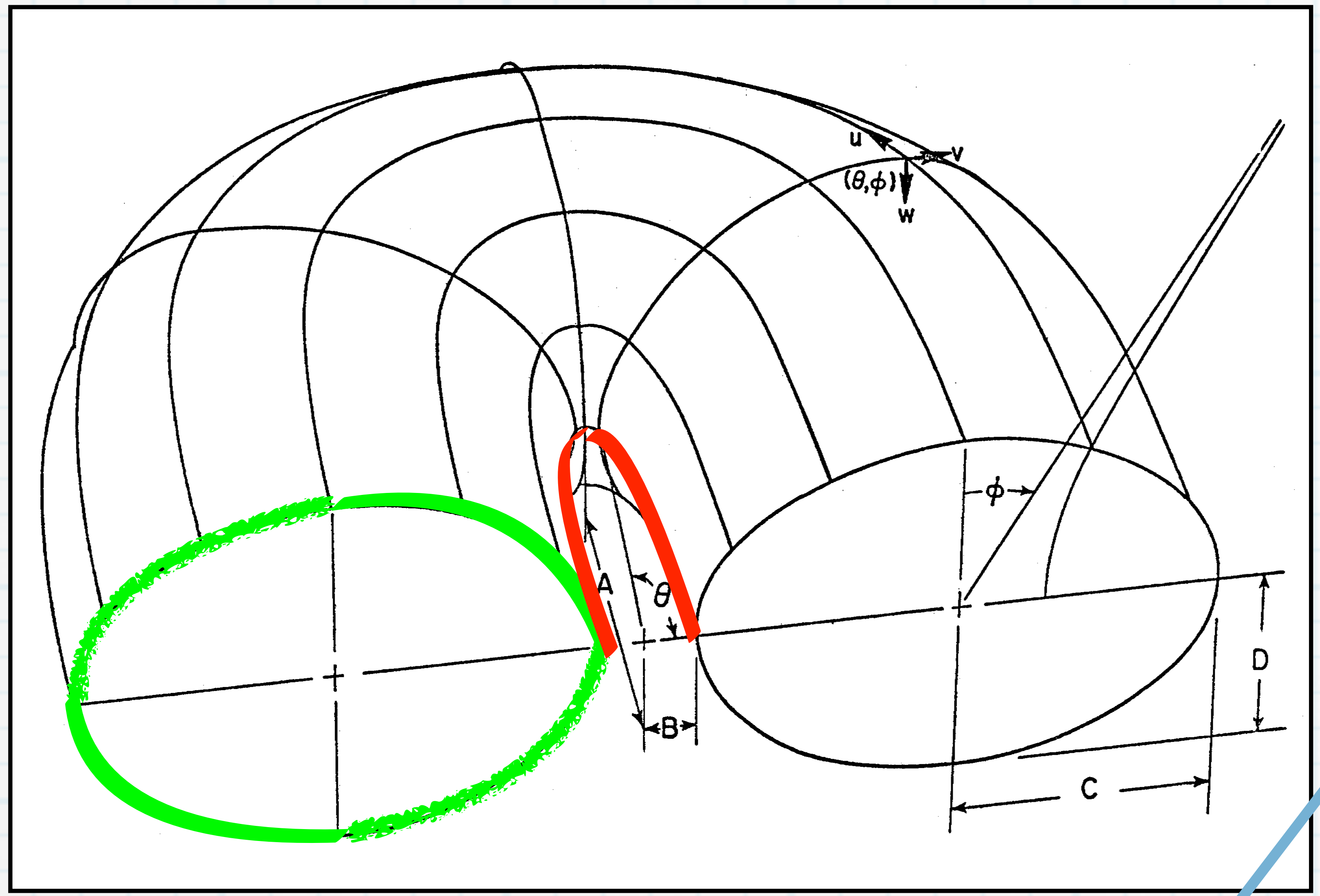
Cooke et al,
1976

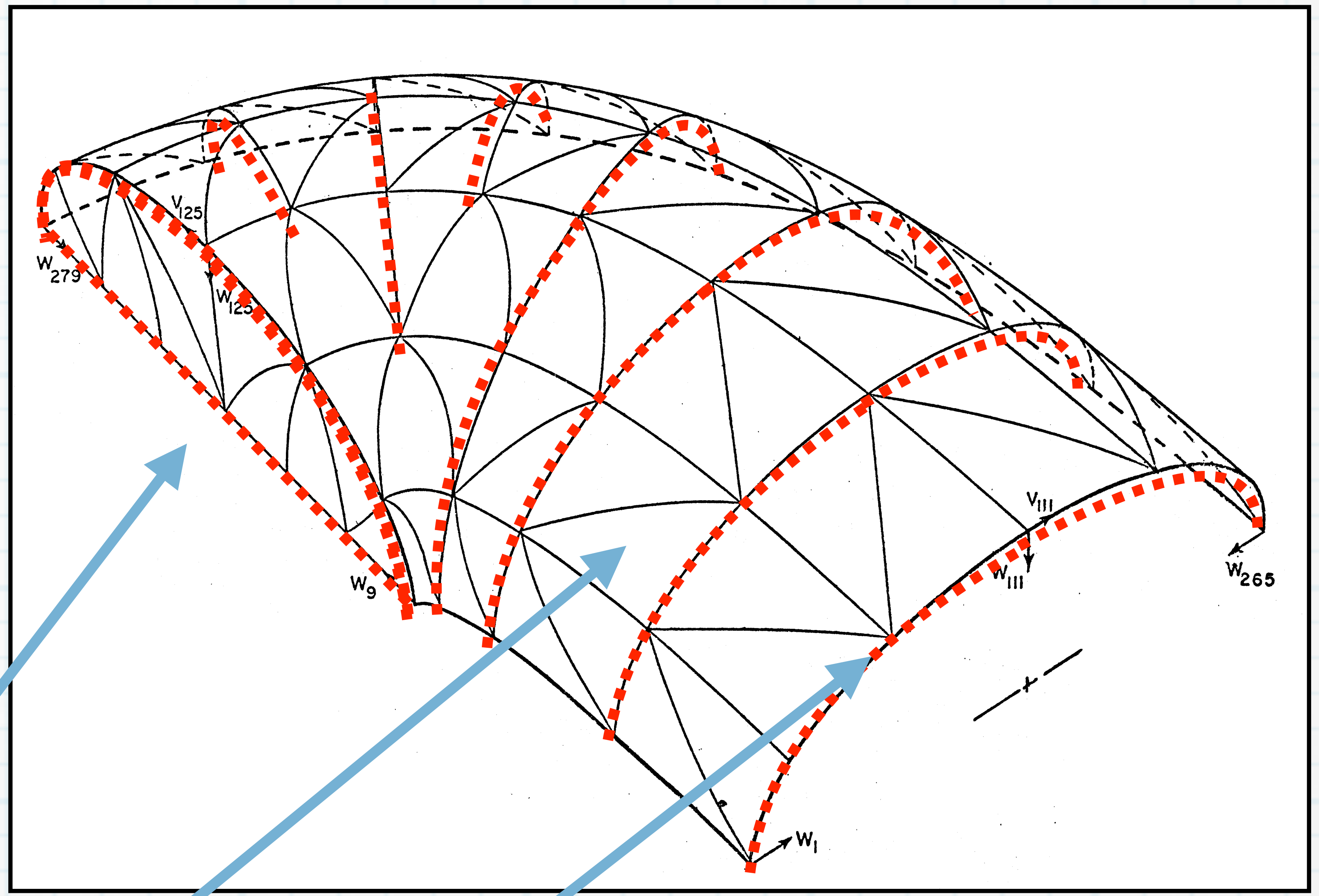
Geometric model

RK-741



Cooke, J.R., J.G. DeBaerdemaeker, R.H. Rand, and H.A. Mang. 1976. A finite element shell analysis of guard cell deformations. Transactions of the ASAE 19(6): 1107-1121.





- This doubly-elliptical geometry was used to represent an elliptical guard cell pair.
- Doubly-curved triangular elements.
- Elements can have radial stiffnesses (micelle theory) different from the orthogonal direction. (Will revisit.)
- The end wall, if present, as is typical, provides stiffening too.

What Determines Pore Size?

The opening and closing of the pore depends upon the opposing pressures of the guard cell and the surrounding cell.

[Translation from von Mohl's 1856 German language paper:]
"Therefore, it is clear that for Amaryllis, the opening and closure of the stomate does not depend solely upon the motion of the guard cells but also upon the antagonism between the guard cells and the epidermal cells."

Opposing Pressures – 1

* Experimental pressure measurements (Edwards, et al., 1976) yielded slopes that are consistent with the computed values [that is, partial derivative values (with the second variable held constant)].

Change in pore width

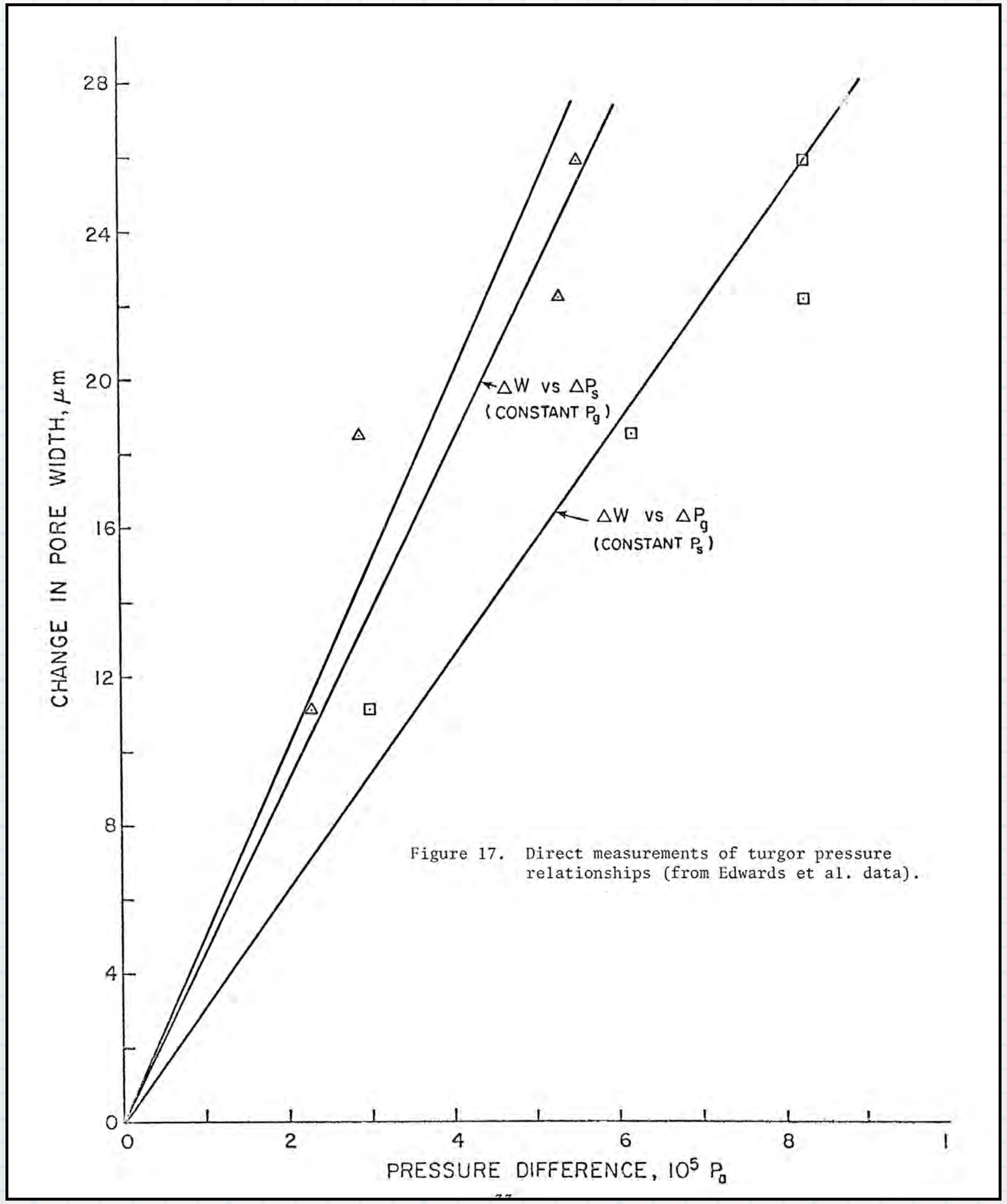


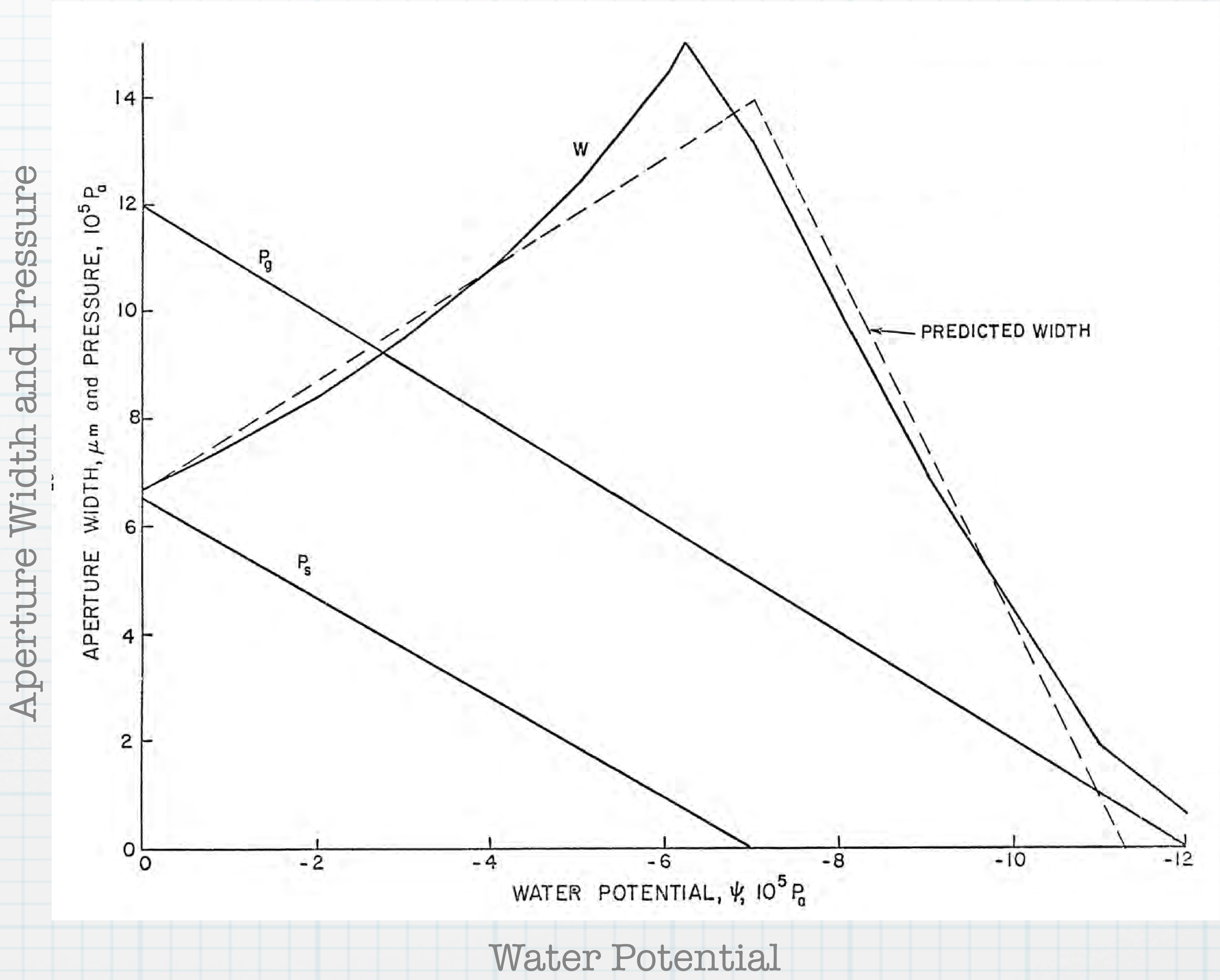
Figure 17. Direct measurements of turgor pressure relationships (from Edwards et al. data).

Pressure Difference

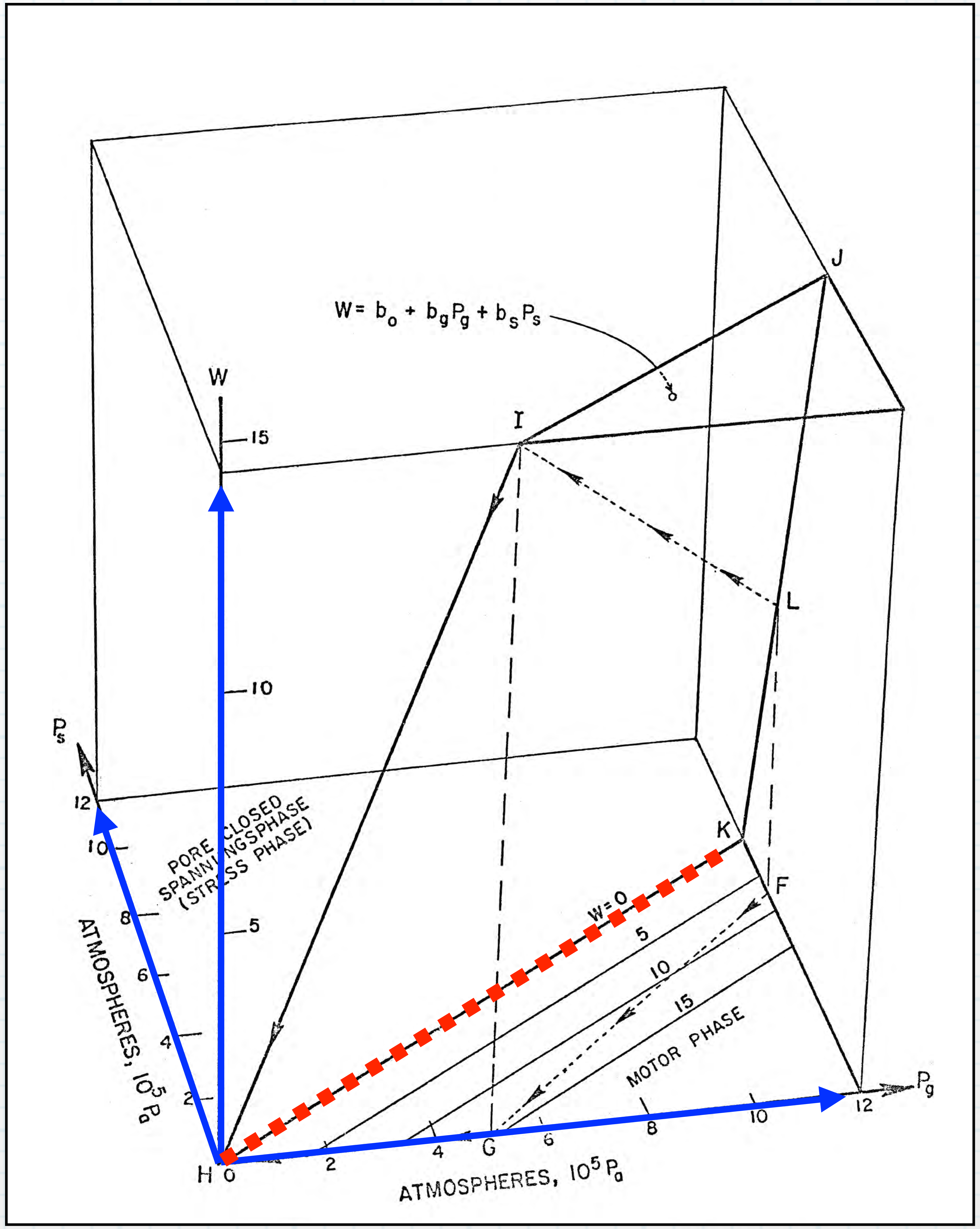
Opposing Pressures – 2

* Glinka's (1971) plasmolytic method results are shown at right.
  The predicted width using our multilinear model is superimposed.

* (A 3-D plot of this follows.)



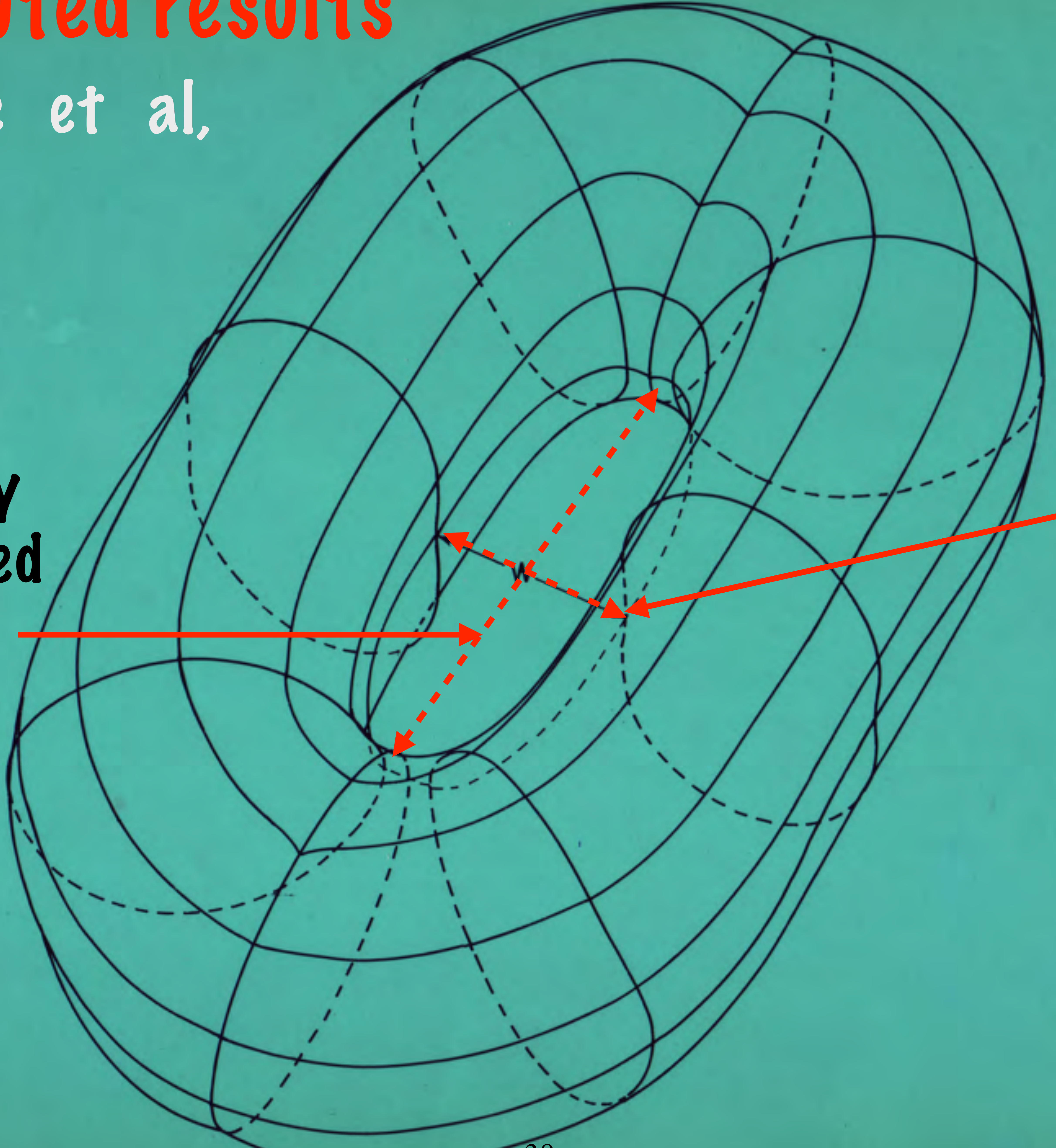
- Predicted **pore width** (vertical axis) is a simple function of the hydraulic pressures
- in the guard cell and
- in the surrounding cell.
- The stress phase and motor phase (in the Pg,Ps plane) have a common boundary at **width equals zero.**



Computed results

Cooke et al, 1976

Pore length remains relatively unchanged despite internal pressure increase.



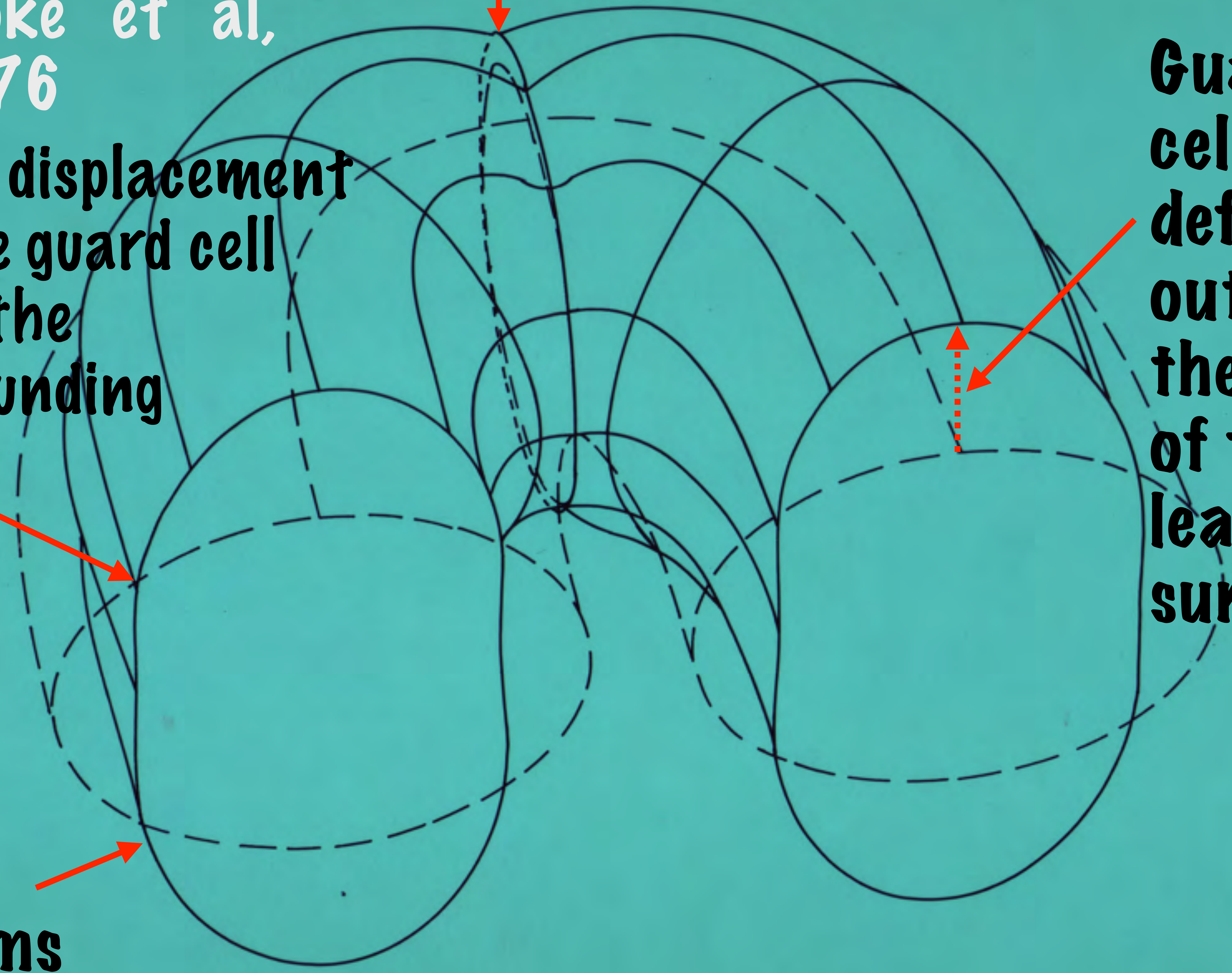
The inner guard cell wall moves outward – increasing pore width – despite the opposing internal pressure increase.

RK-742

Computed results

Cooke et al, 1976

Guard cell deforms less at the ends where two cells join.



Little displacement where guard cell joins the surrounding cell.

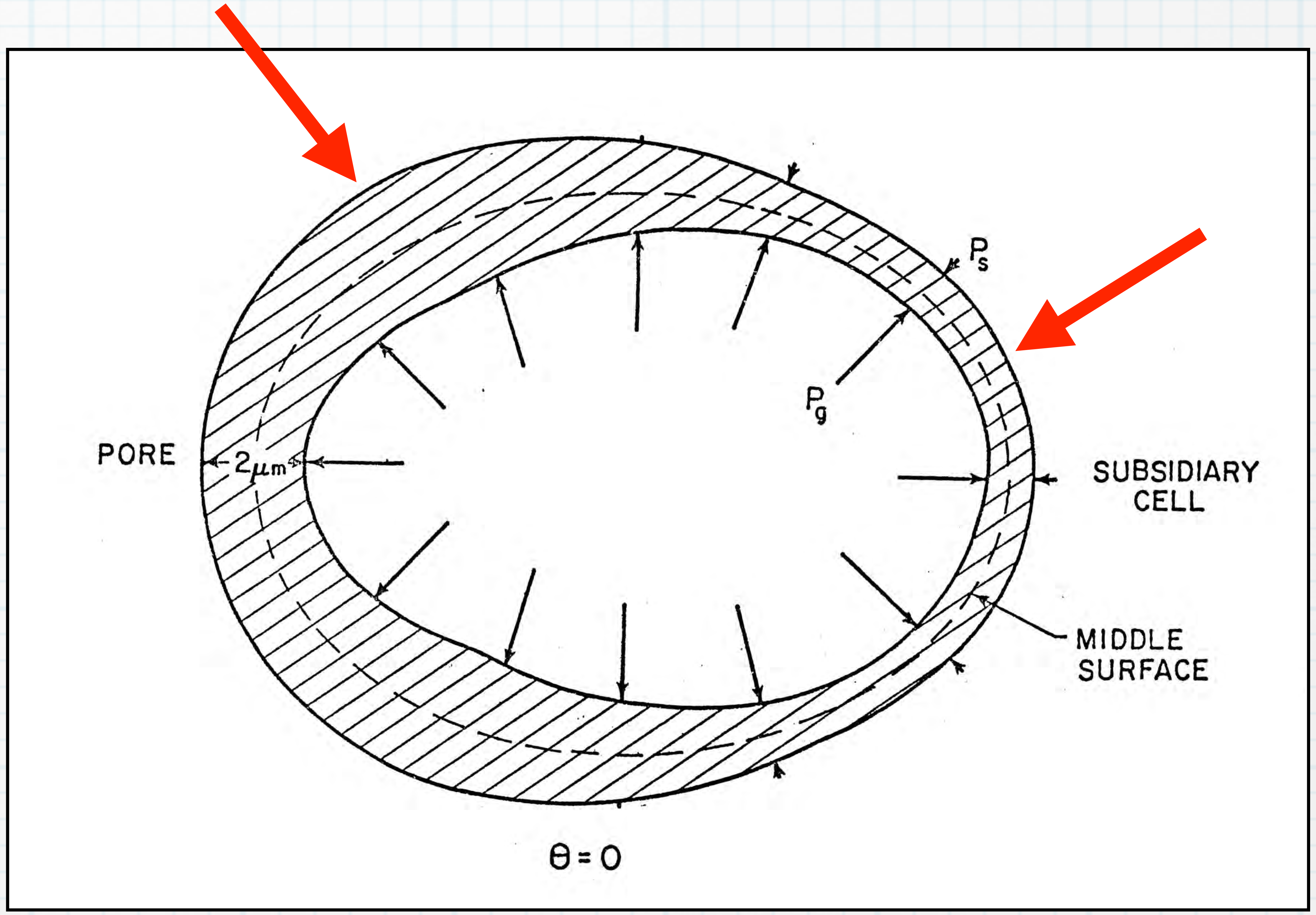
Guard cell deforms out of the plane of the leaf surface.

Guard cell deforms by bending, rather than by stretching (less ATP).

RK - 740

Wall Thickness

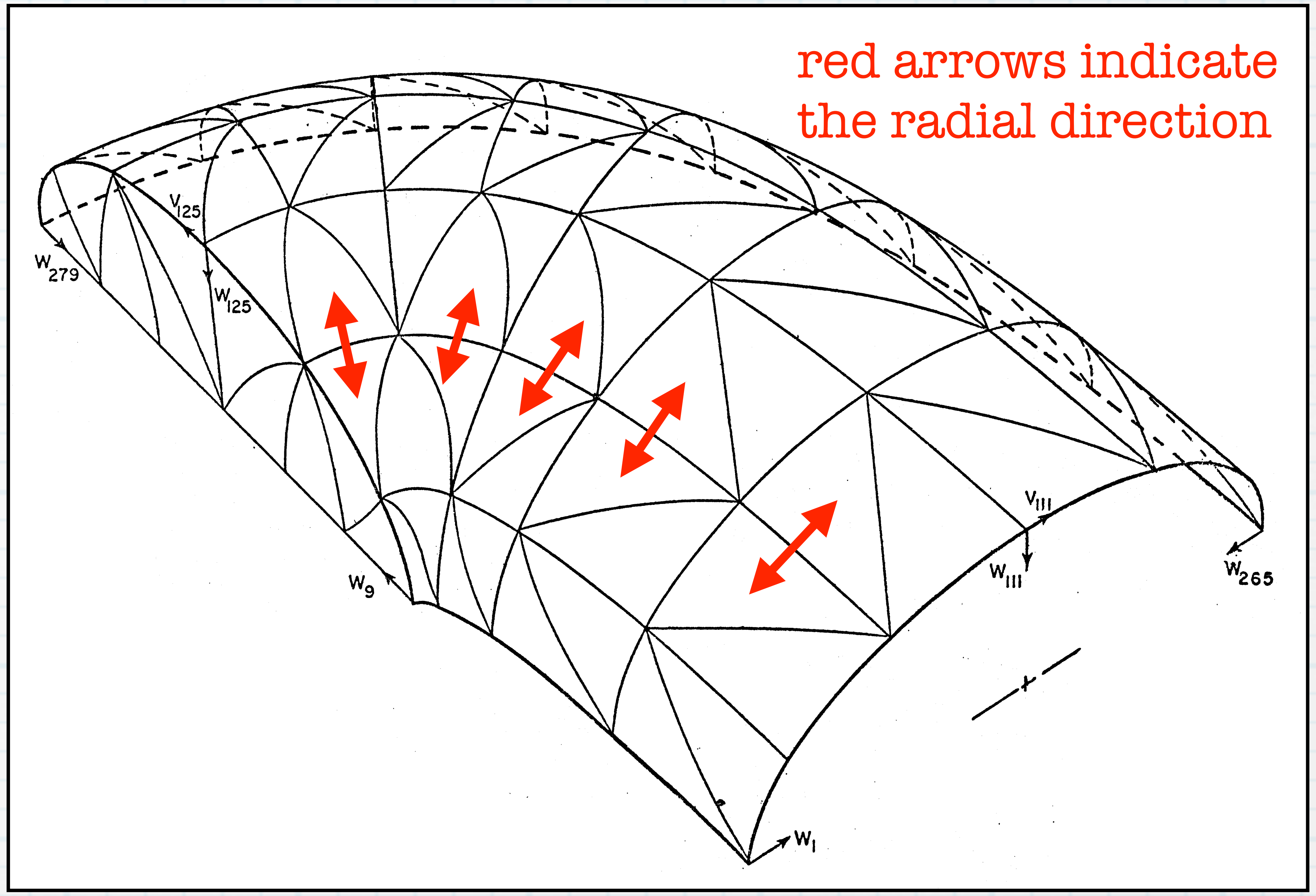
* Variable wall thickness of the guard cell is not a major factor for pore opening, i.e., is not central as has been widely believed.



[Although shell thickness variations do affect guard cell deformation, the presence of a "thick" ventral wall and a "thin" dorsal wall do NOT appear to be essential structural aspects of pore openings.]

Micelle – 1

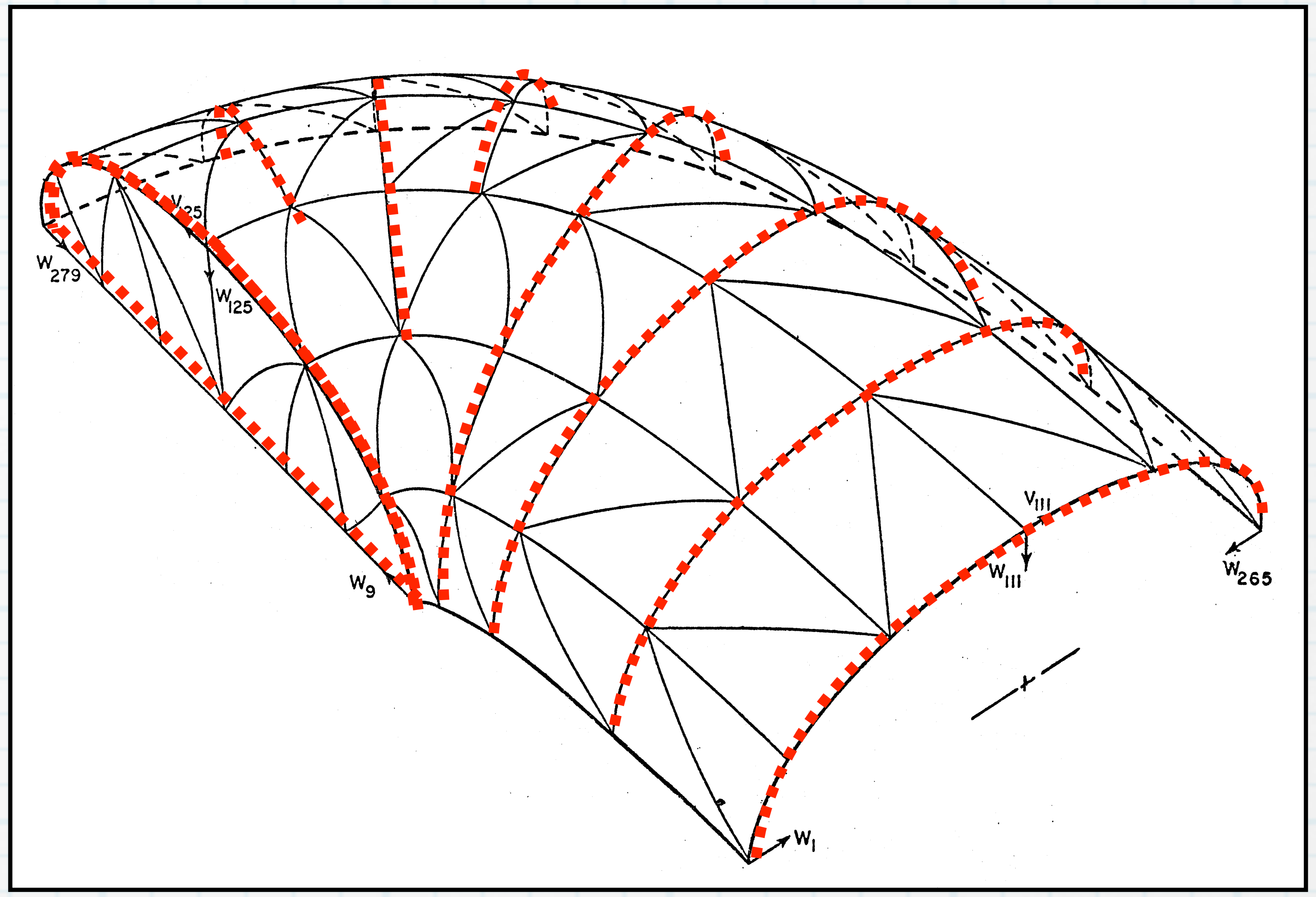
Cellulose microfibrils are arranged **radially** in guard cells, making the wall stiffer in the radial direction, than in the orthogonal direction.



* Even if NO micelle were present (in a sufficiently thick doubly-elliptical guard cell), pore width increases with an increase in guard cell pressure.
* Also with no micelle, the pore width increase due to a given guard cell pressure increase would be offset by the same surrounding cell pressure increase.

Micelle - 2

* The effect of the micelle in the guard cell is represented by an increase in Young's Modulus in the radial direction (red lines) with respect to the orthogonal direction. [That is, we're treating this as an anisotropic elastic material.]



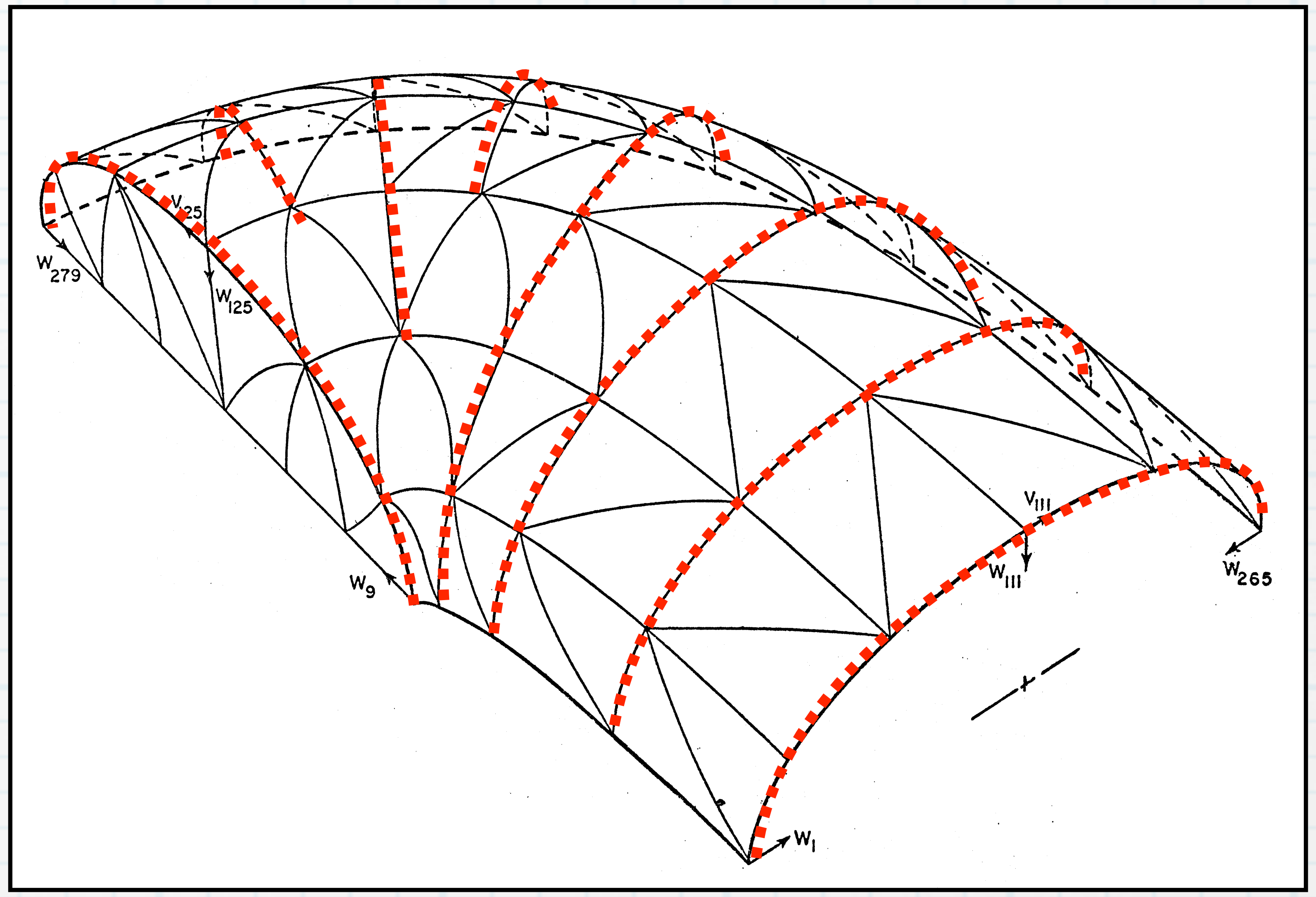
* IMPORTANTLY, the micelle increase the influence of the (smaller) pressure changes in the surrounding cell. [This CRUCIAL role of the micelle will become clearer in the next chapter.]

* In addition to the radial stiffening by micelle, the tensile properties of the end-walls (where two guard cells join) contribute to this stiffening!

Micelle – 3

Micelle Determine the Antagonism Ratio

Micelle Anisotropy (Young's Modulus ratio)	1	5	10
Antagonism ratio	-0.98	-1.55	-1.90
Ratio of the Surrounding Cell Pressure Change to Offset the Guard Cell Pressure Change	1.02	0.65	0.53

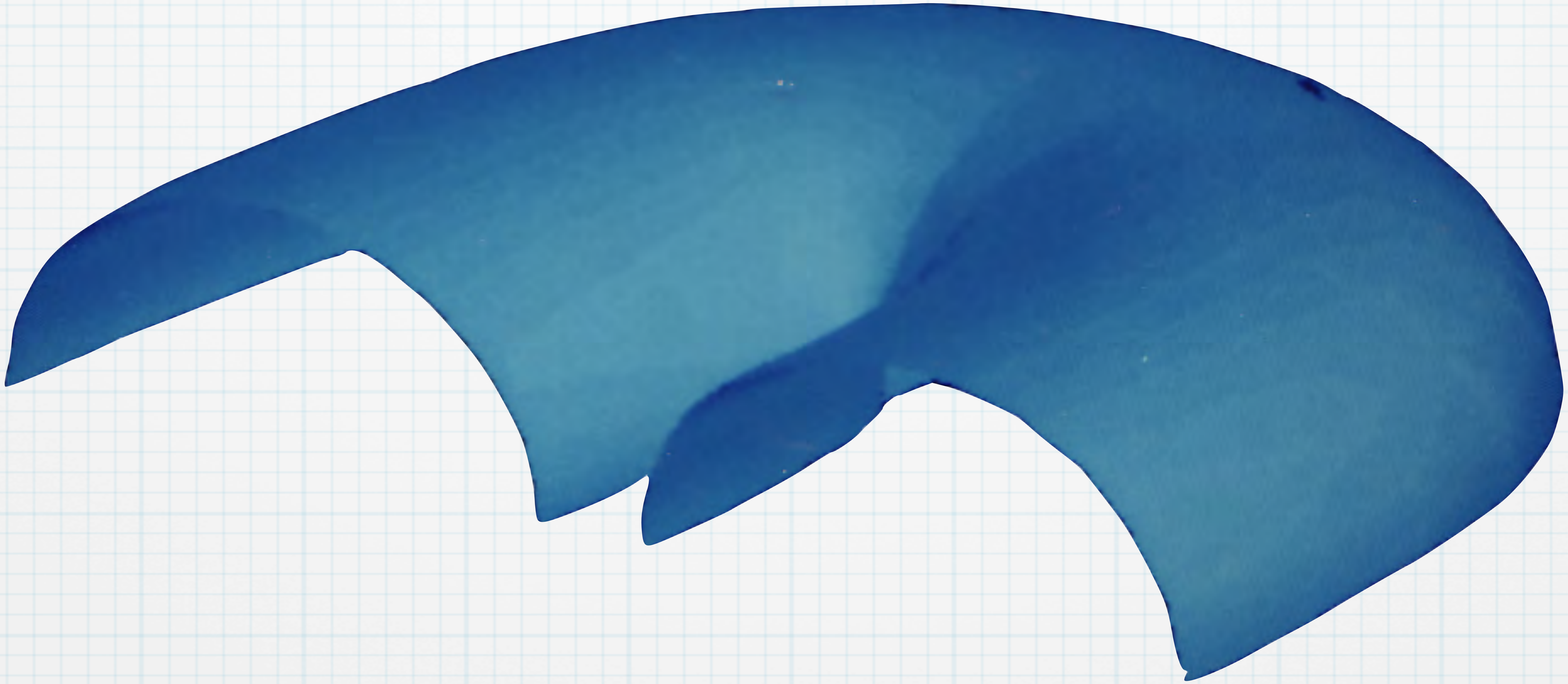


Antagonism Ratio: An increase in guard cell pressure increases the pore width, but an increase in the surrounding cell pressure decreases the pore width. This "antagonistic" effect, observed in 1856 by von Mohl, can be quantified as an antagonism ratio. **Anisotrophy** = ratio of Young's Modulus in direction of micelle to Young's Modulus in the orthogonal direction. The last row of the table is the negative reciprocal of the antagonism ratio. Wall thickness = 2 microns.

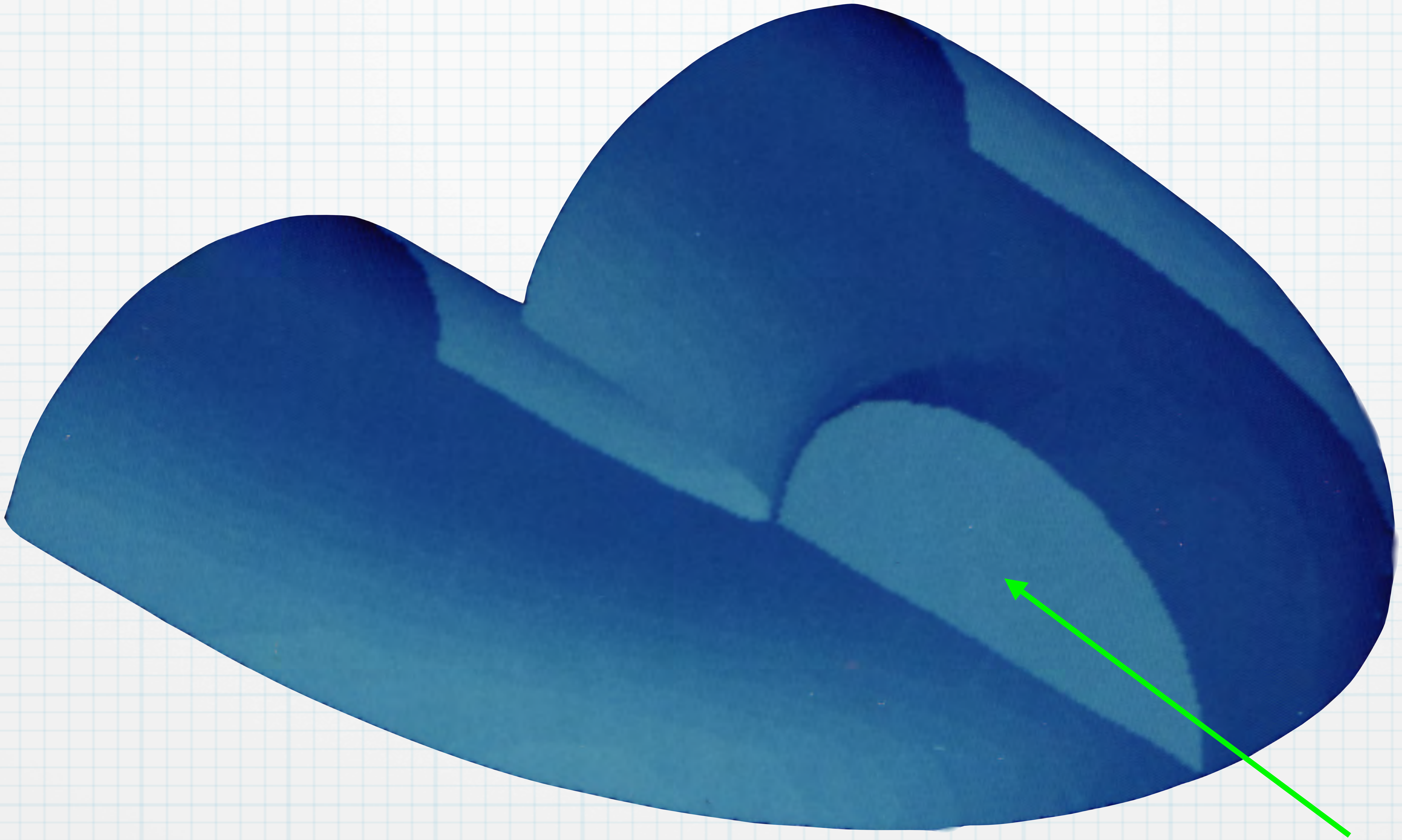
Pore width is determined by the opposing, i.e., "antagonistic" guard cell and surrounding cell pressures.

Due to micelle, a pore width increase due to a unit change in guard cell pressure might be offset by only half that same pressure change in the surrounding cell.

Lee, 1986

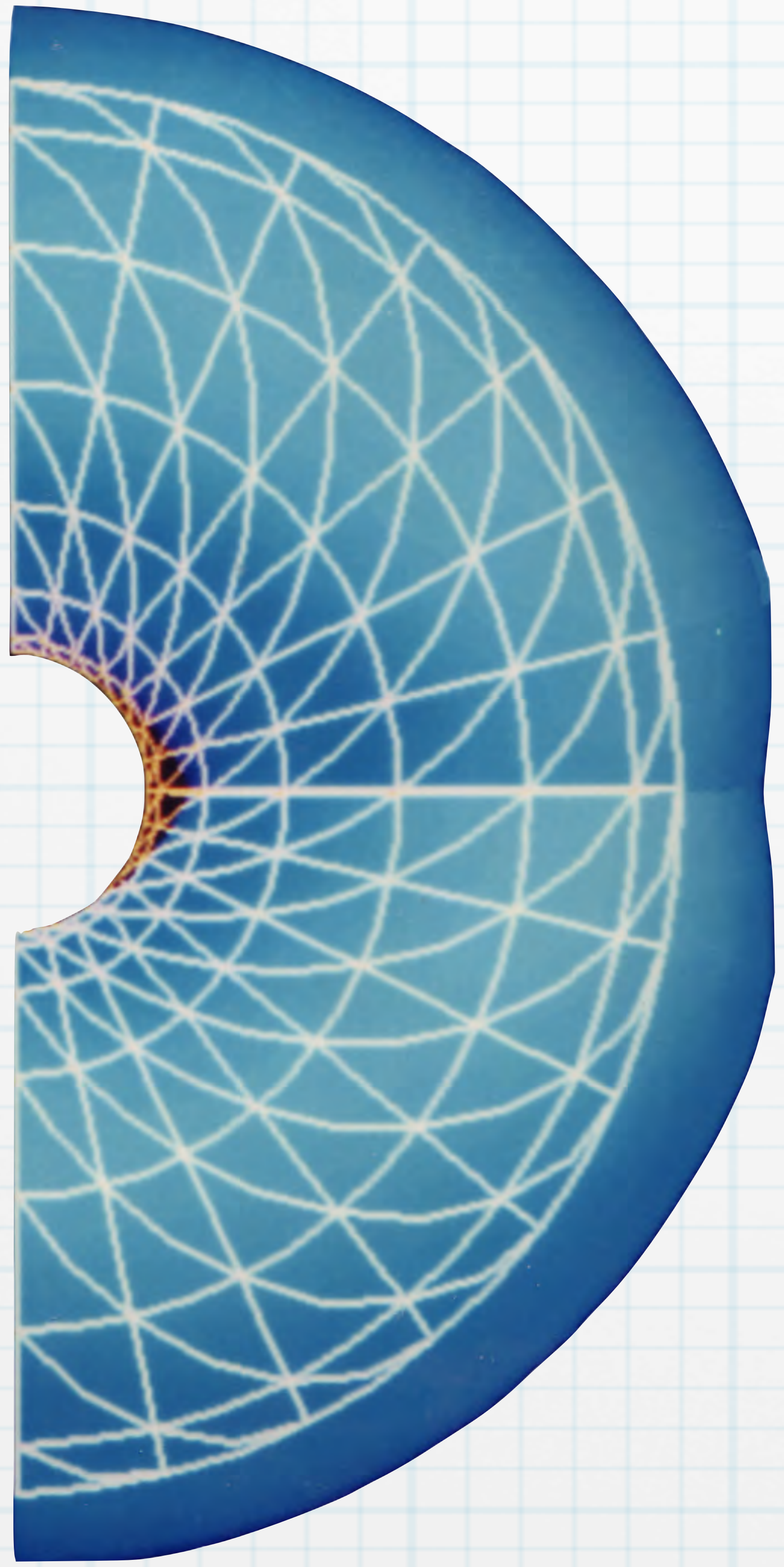


Lee, Jae Young. June 1986. A Finite Element for Shell Analysis and Its Application to Biological Objects. PhD Dissertation, Cornell University. https://hdl.handle.net/1813/45413

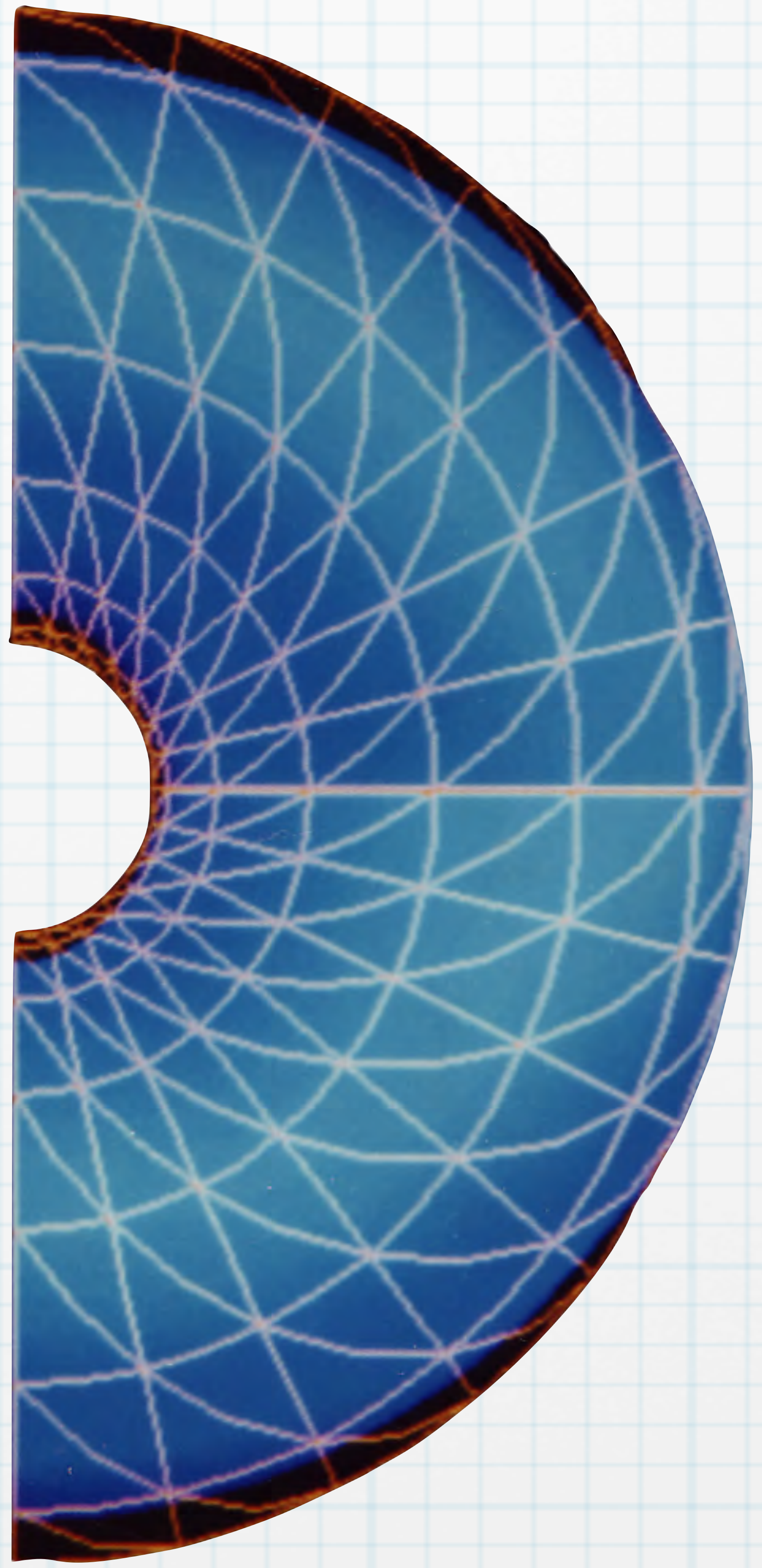


At the end of the guard cell pair, a common wall exists (and stiffens the shell in that radial direction).

Circular torus geometry for a mature guard cell doesn't work.
(Pore should open if inflated and close under water deficit.)



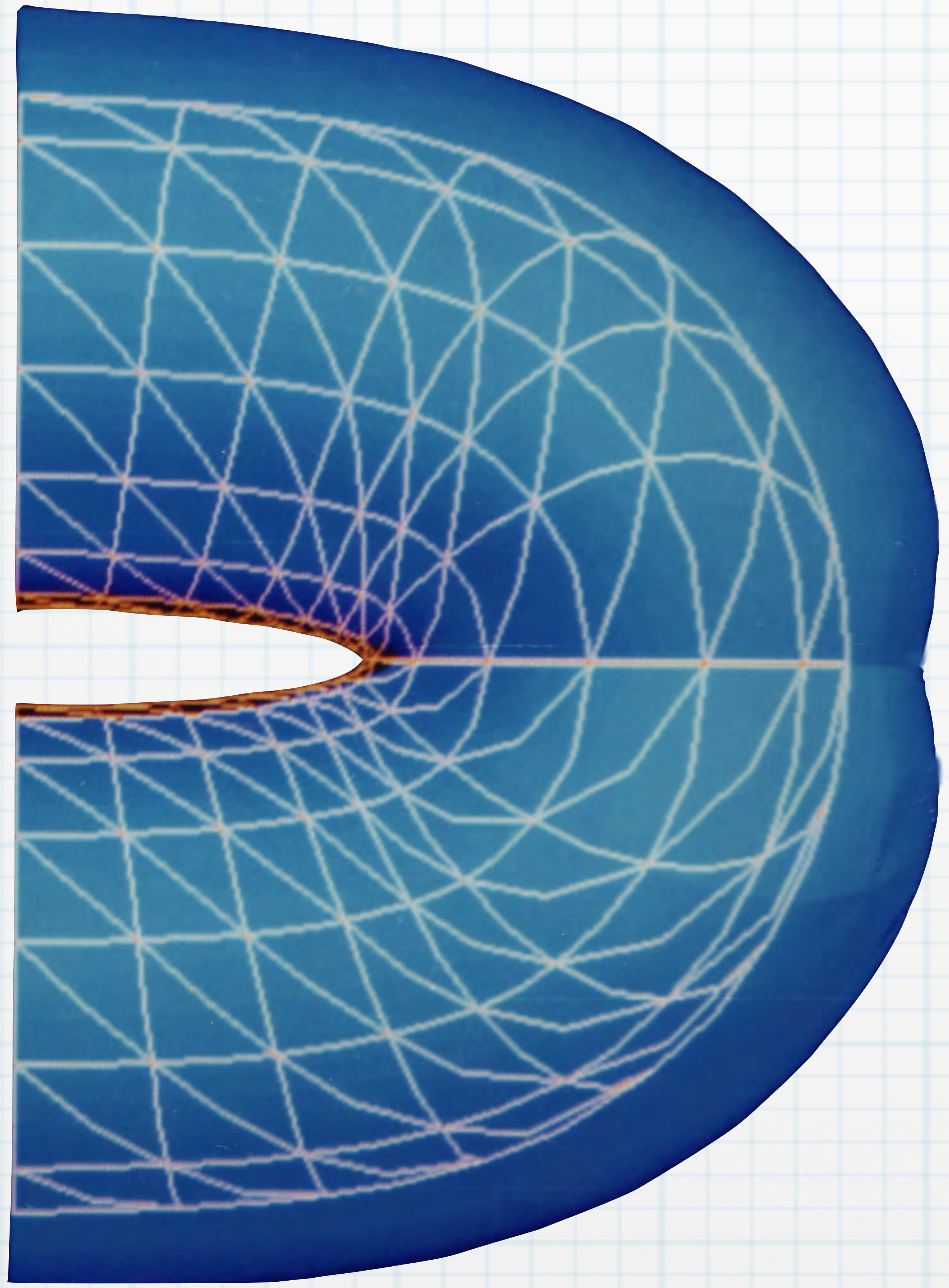
Circular plan (external) view; circular elevation



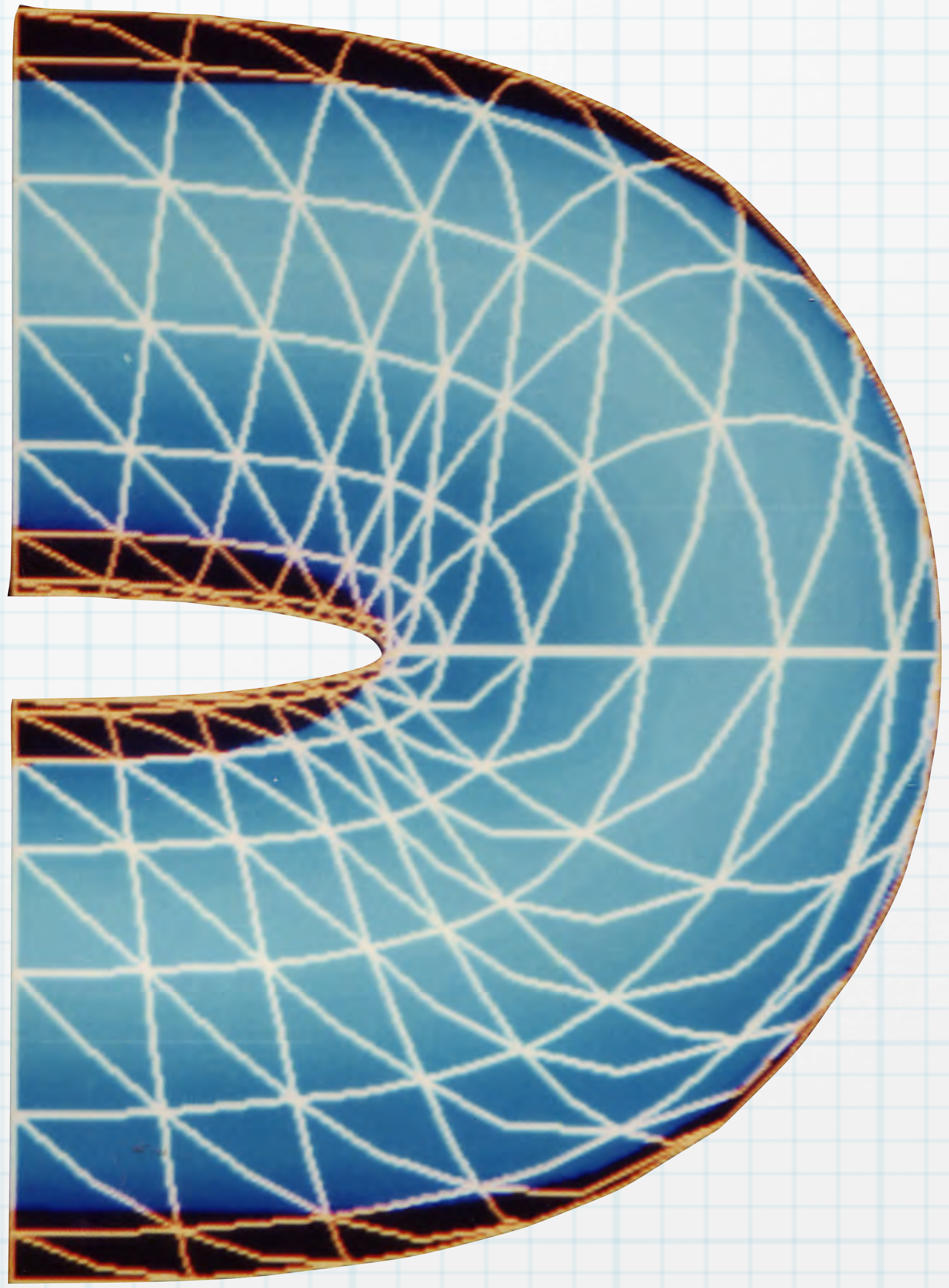
Circular plan (external) view; elliptical elevation

(both with a plate at the end)

An elliptical torus geometry **does** work (pore opens when inflated).



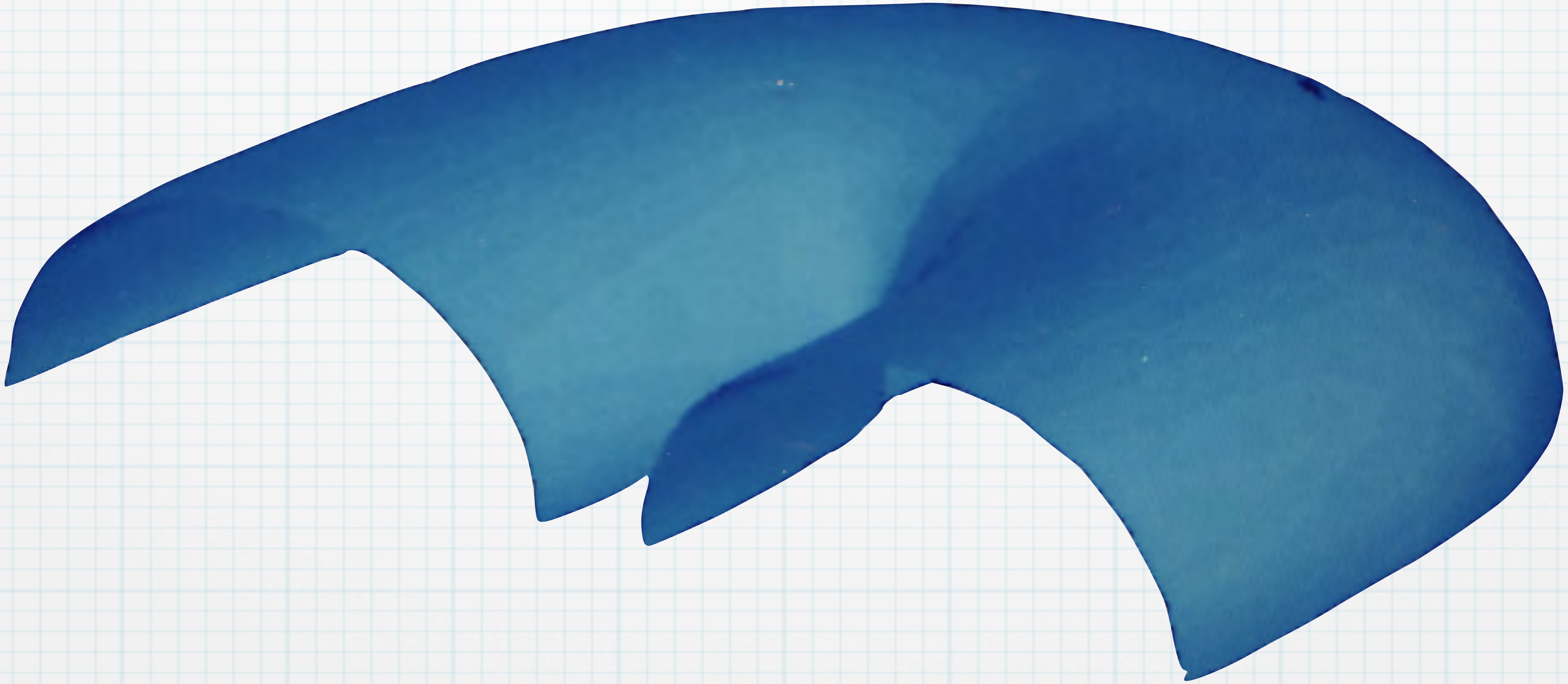
Elliptical plan; circular elevation



Elliptical plan; elliptical elevation

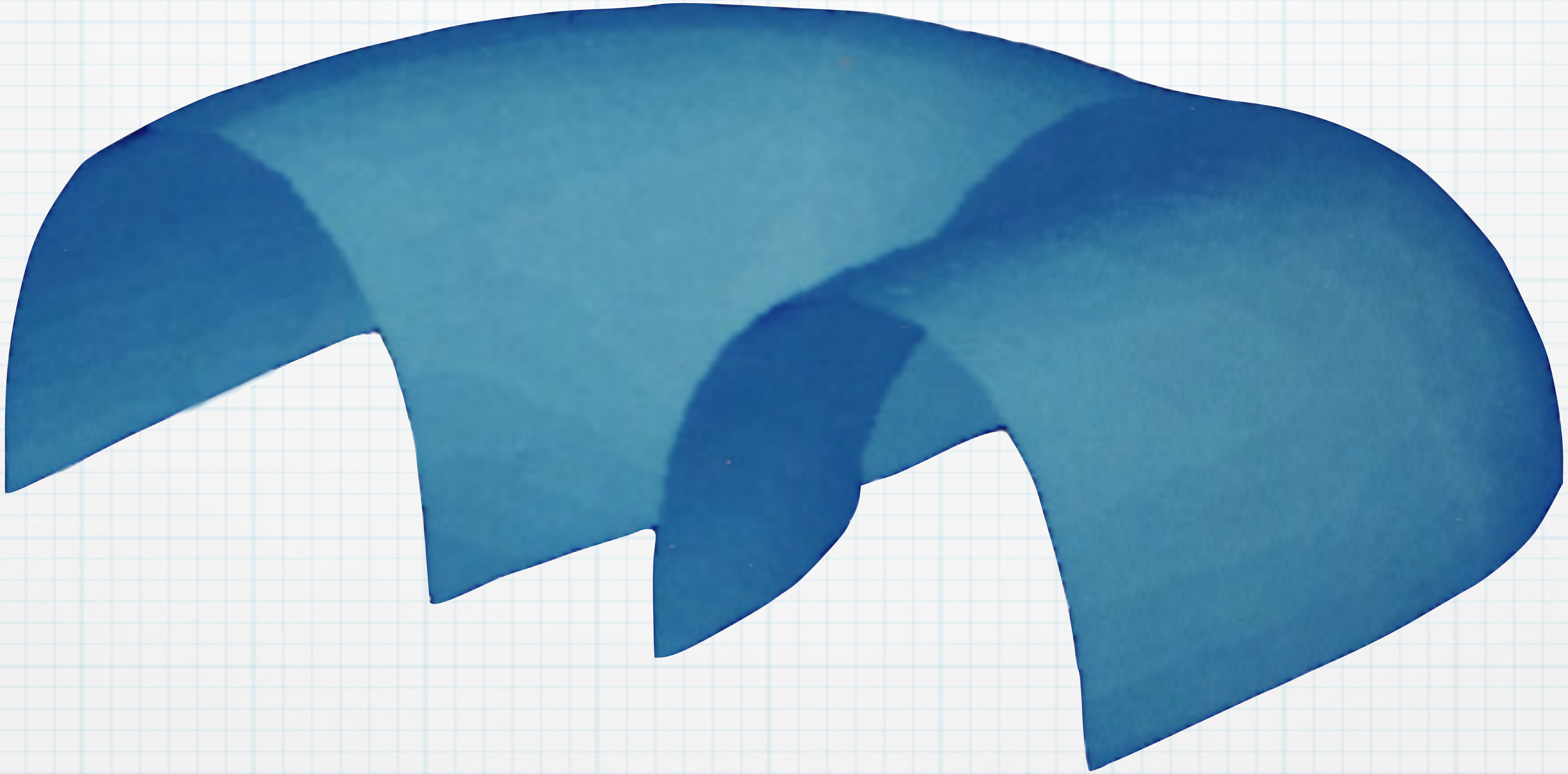
(both with a plate at the end)

Lee, 1986 (again)

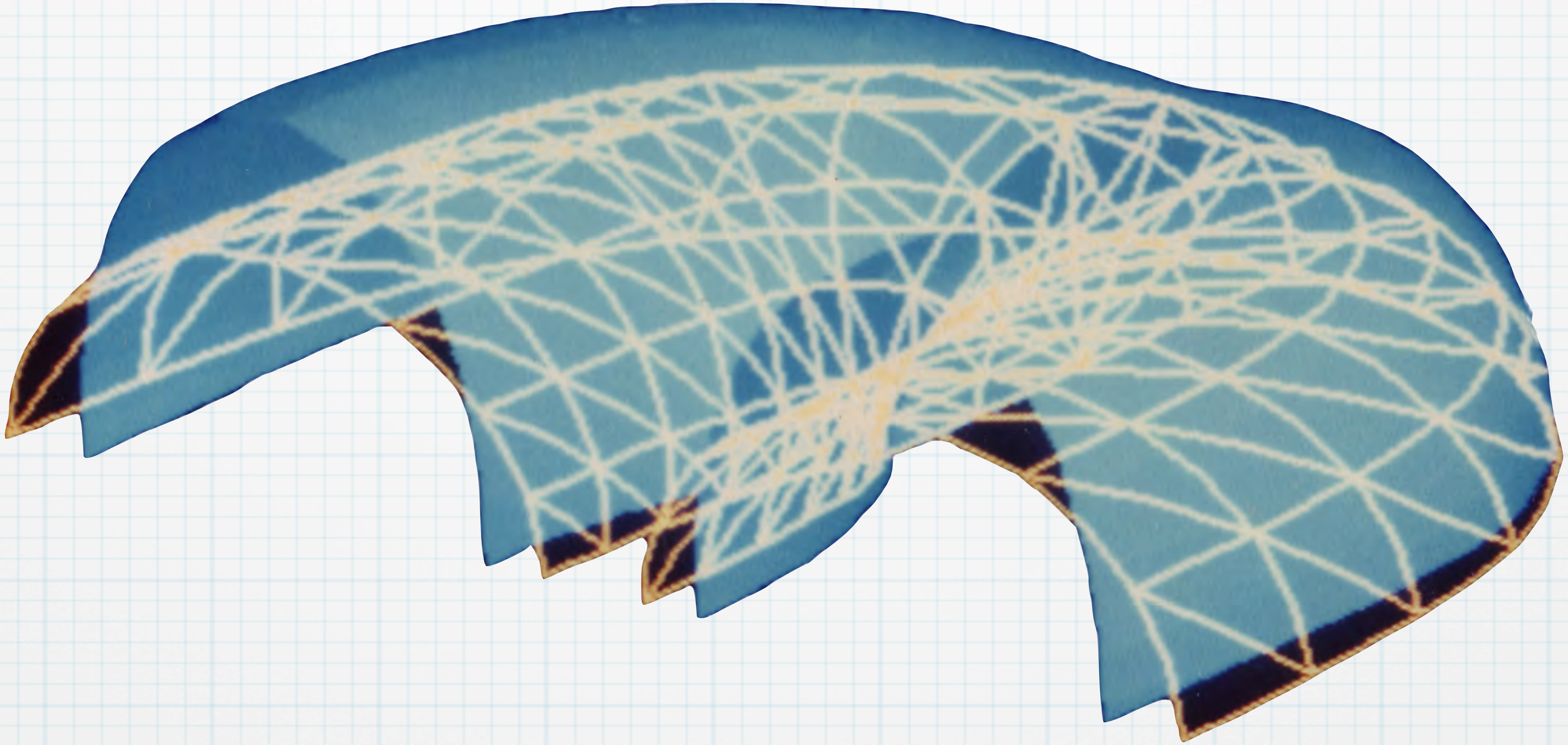


undeformed

Lee, 1986

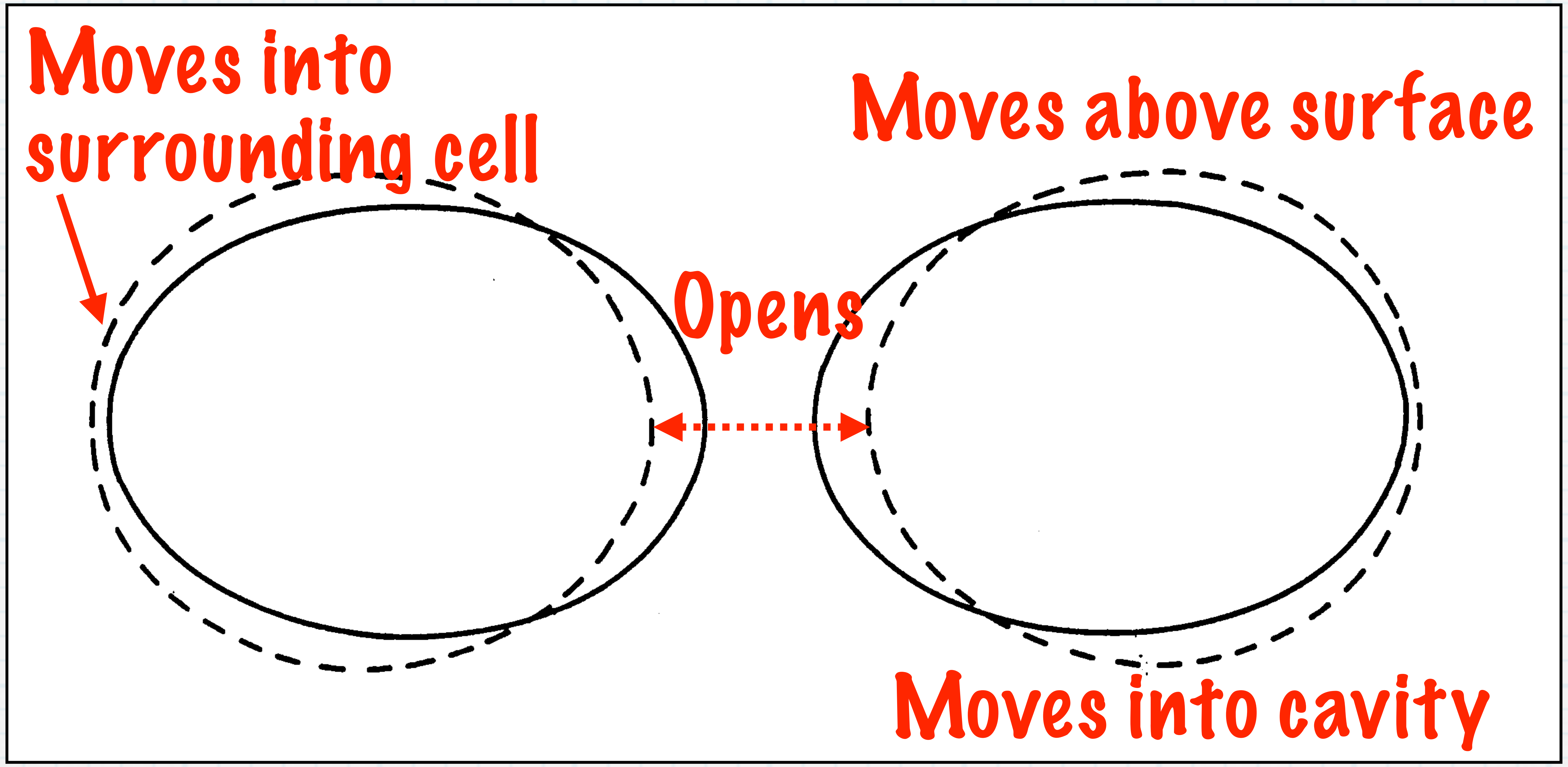


Deformed Shape

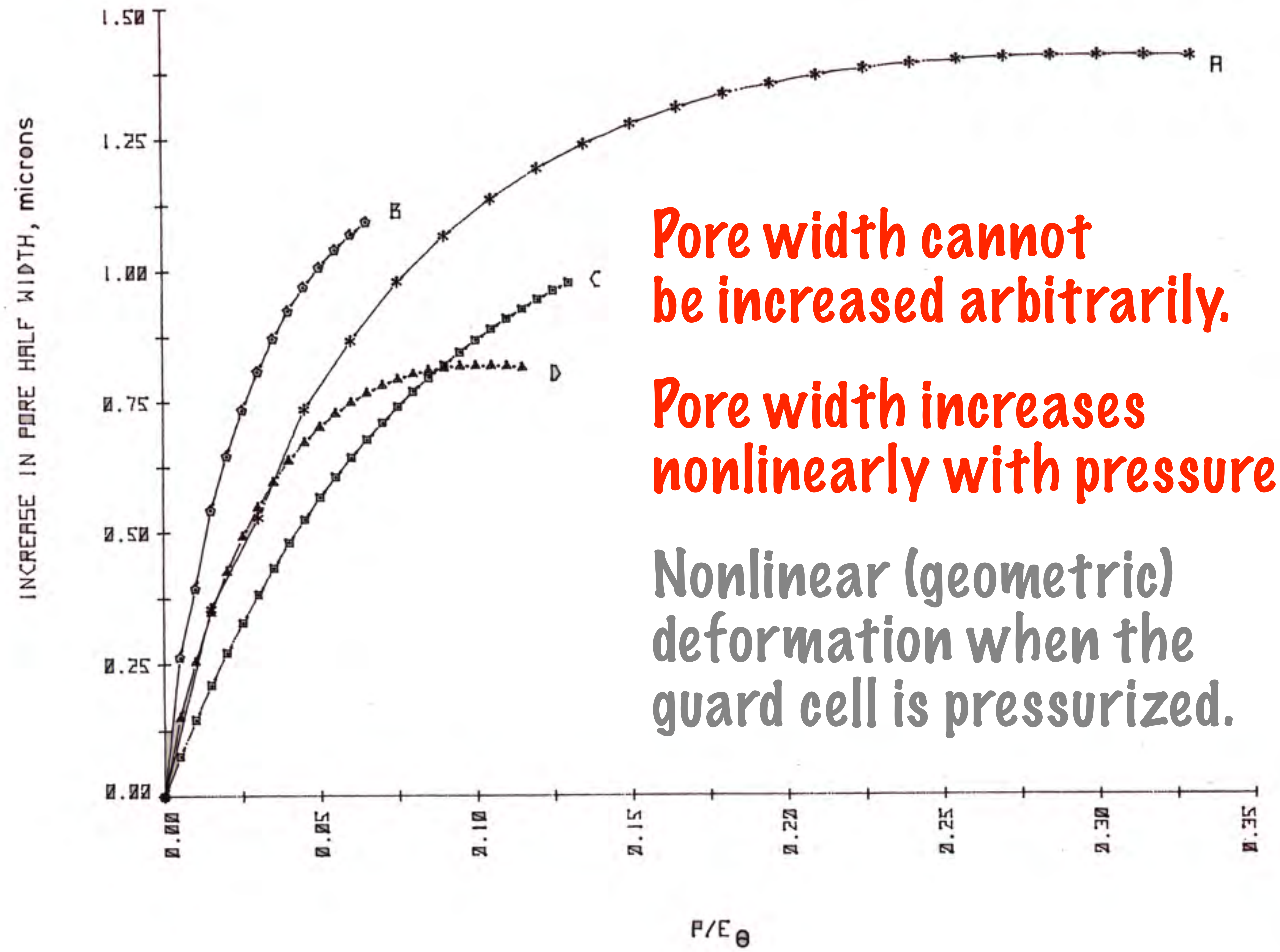


Deformed and undeformed

Nonlinear Deformation



* Nonlinear (geometric) deformations (solid - undeformed; dashed - deformed)
* Pore opens,
* guard cell moves above epidermis and into the cavity,
* and protrudes into the surrounding cell.



Pore width cannot be increased arbitrarily.

Pore width increases nonlinearly with pressure.

Nonlinear (geometric) deformation when the guard cell is pressurized.

Cooke, J.R., R.H. Rand, H.A. Mang, and J.G. DeBaerdemaeker. 1977. A nonlinear finite element analysis of stomatal guard cells. ASAE Paper No. 77-5511. 18 pages.

The Geometrically Nonlinear Model

(Pore width vs normalized internal pressure)

* With increasing pressure, the pore width increases in a nonlinear manner and plateaus, i.e., the width cannot be increased arbitrarily.
* Decreasing wall thickness increases the pore size for a given pressure.
* The greater the stiffness provided by the micelle, the greater the maximum pore width achievable.

Conclusions
(Structural Mechanics - 1)

* The dominant consideration is geometry:
  * A standard, circular torus shell does not respond appropriately to a pressure increase in the guard cell,
  * But a sufficiently thick, doubly-elliptical shell model does respond appropriately, even with uniform wall thickness.
  * An elliptical torus - even if perfectly isotropic (i.e., without micelle) - will open under increasing hydrostatic pressure, but the micelle do improve its structural response. [However, as described in the next chapter, micelle play a **CRUCIAL** role in the time-dependent system response.]

Conclusions

(Structural Mechanics - 2)

* Stomatal opening and closing depend inherently upon the opposing interaction (antagonism) of the guard cell and adjacent epidermal cells, as suggested by von Mohl in 1856.
* The pore length remains relatively constant during opening and closing. [This property was not included a priori as an assumption.]
* Although shell thickness variations do affect guard cell deformation, a "thin" dorsal wall and a "thick" ventral wall do not explain the structural aspects of stomatal opening.

Conclusions
(Structural Mechanics - 3)

* The experimental results of Glinka, who used a plasmolytic technique, and Edwards, Meidner and Sheriff, who used a direct pressure measurement technique, are reinterpreted and are shown to be in harmony with this analysis.
* The Spannungsphase (stress phase) behavior of stomates is shown to occur in an identifiable, triangular region of the Pg-Ps plane.
* When geometrical nonlinearity is included in the analysis, the pore cannot be made arbitrarily larger.
* As will be shown in Part 3, the micelle (radial stiffening) becomes a crucial factor for the dynamical response of the stomatal system.

Stomatal System Dynamics

Part 3
Transient & Periodic

Review - 3
(structural)

In the previous chapter (using a doubly-elliptical torus model), we examined the structural aspects of kidney-shaped guard cells.

We examined the role of
geometry, wall thickness, and micelle.

- **GEOMETRY is a dominant issue:**
  - Elliptical geometry is central. [A circular torus does not work.]
  - Doubly-elliptical geometry would work (static case) - even with uniform wall thickness and without radial stiffening.
    - That is, a variable wall thickness is not the primary basis for stomatal pore opening, as widely believed.
    - Further, micelle are not essential to obtain structurally appropriate pore openings, but do enhance pore opening.

Review - 4
(structural)

- [However, as will be detailed in this chapter, micelle play a crucial role in the time-dependent response.]

- The stomate's stress and motor phases were given an explicit interpretation.
- The pore length remains relatively constant during opening and closing; this property need not be included a priori as an assumption.
- The guard cell deforms out of the plane of the leaf (mostly by bending), and
- The other cells on the leaf surface should experience only limited stretching when the guard cell opens (because the guard cells deform mostly out of the plane of the leaf).

Let's now consider how the parts of the stomatal system interact. We'll examine both the transient and oscillatory responses.

Puzzlement - 3

(system)

The opposing hydrostatic pressures within the guard and surrounding cells determine stomatal pore width. These two pressures (for hydropassive conditions) **are established by the movement of water between these cells and within other parts of the stomatal system.**

What is the role of the micelle in the guard cell in shaping the dynamical response of the stomatal system?

Puzzlement - 4

(system)

What water transport scenario within the stomatal system might cause a pore to open?

Under certain stressful, but PERFECTLY CONSTANT environmental conditions, stomatal pores can open and close <u>repetitively</u>? How can this be?

Stoma Opening Video
(Experimental – using microscope)

Source: probably K. Raschke

[1]

[2]

[3]

[4]

Stoma Opening (light microscope)

(Source: probably K. Raschke)

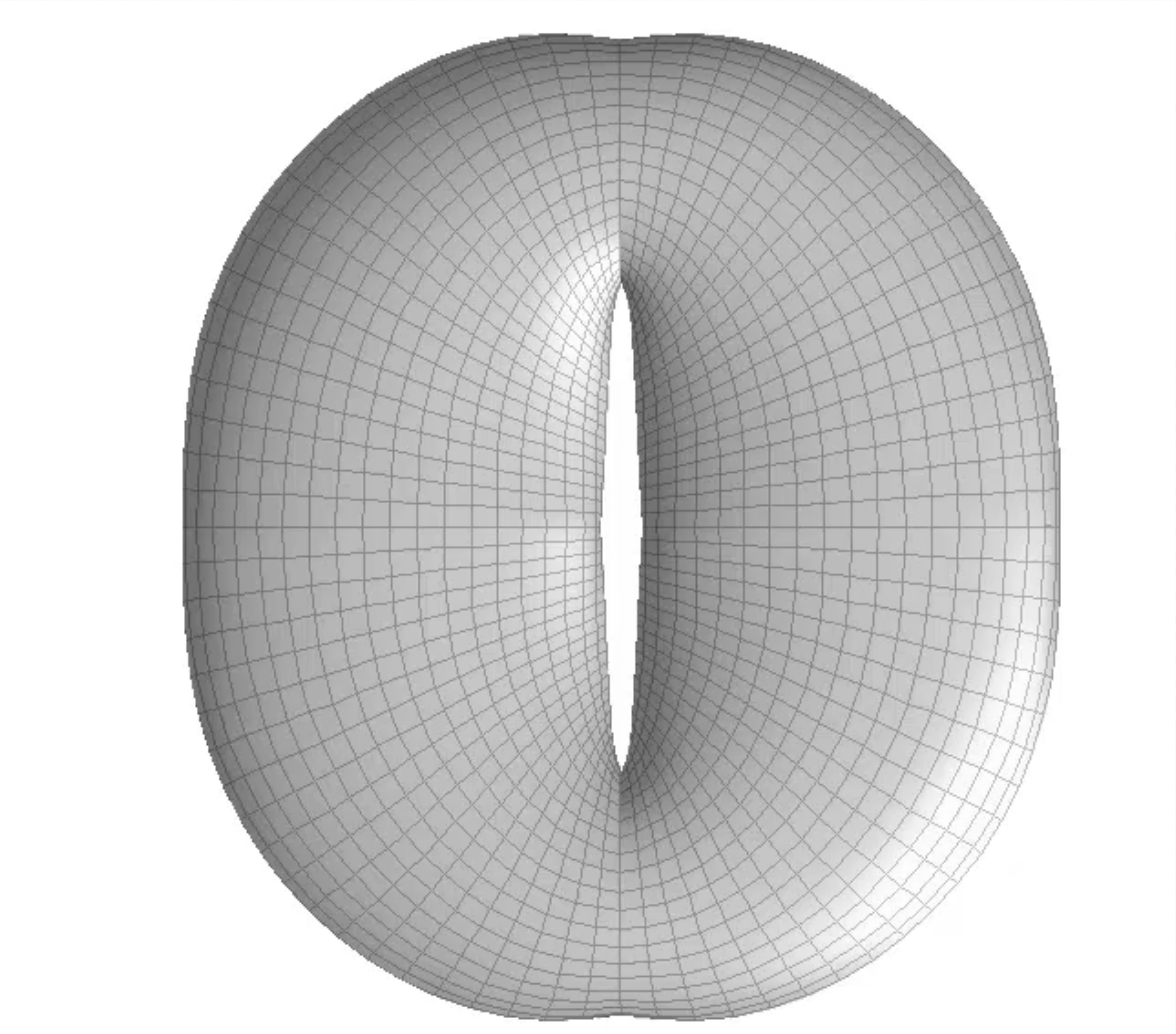
Animations
(using VisualFEA)

Two animations of the opening and closing of a stoma follow:

1. Thin elastic shell (linear)
2. Thick anisotropic shell (linear)

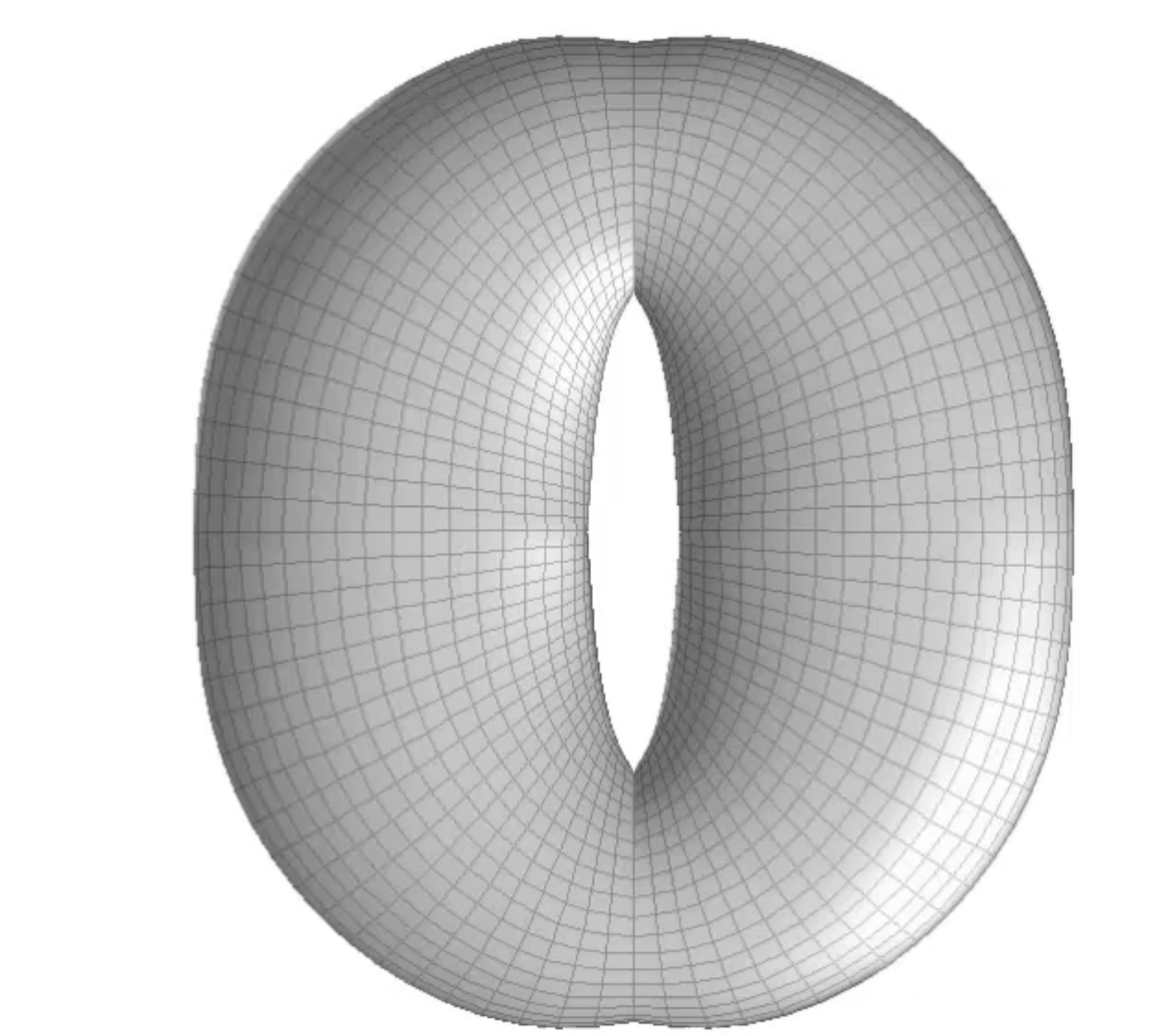
Some Applications of VisualFEA by Jae Young Lee
https://ecommons.cornell.edu/handle/1813/43791

Animation: Shell Model using VisualFEA (Jae Young Lee, 2008)



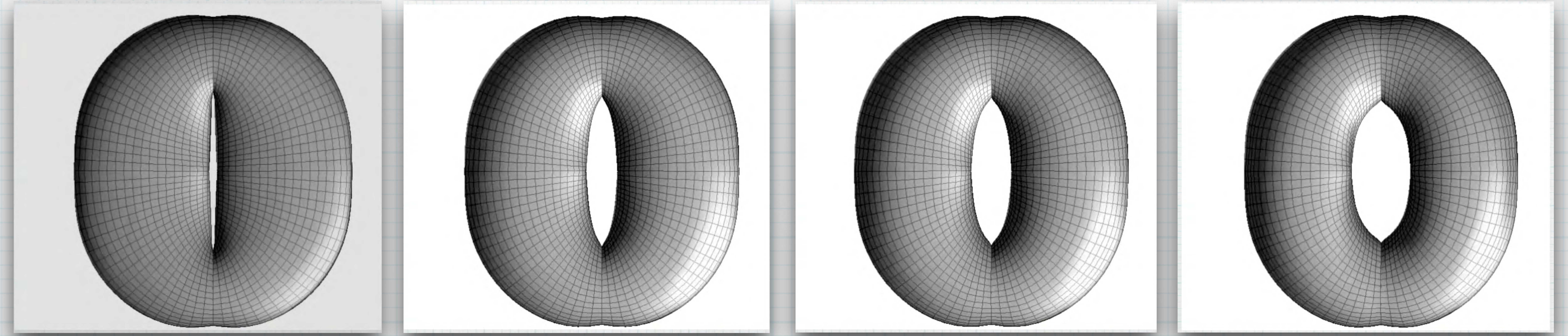
This video is also available online at http://hdl.handle.net/1813/43793

Animation: Solid Anisotropic Model using VisualFEA (Jae Young Lee, 2008)



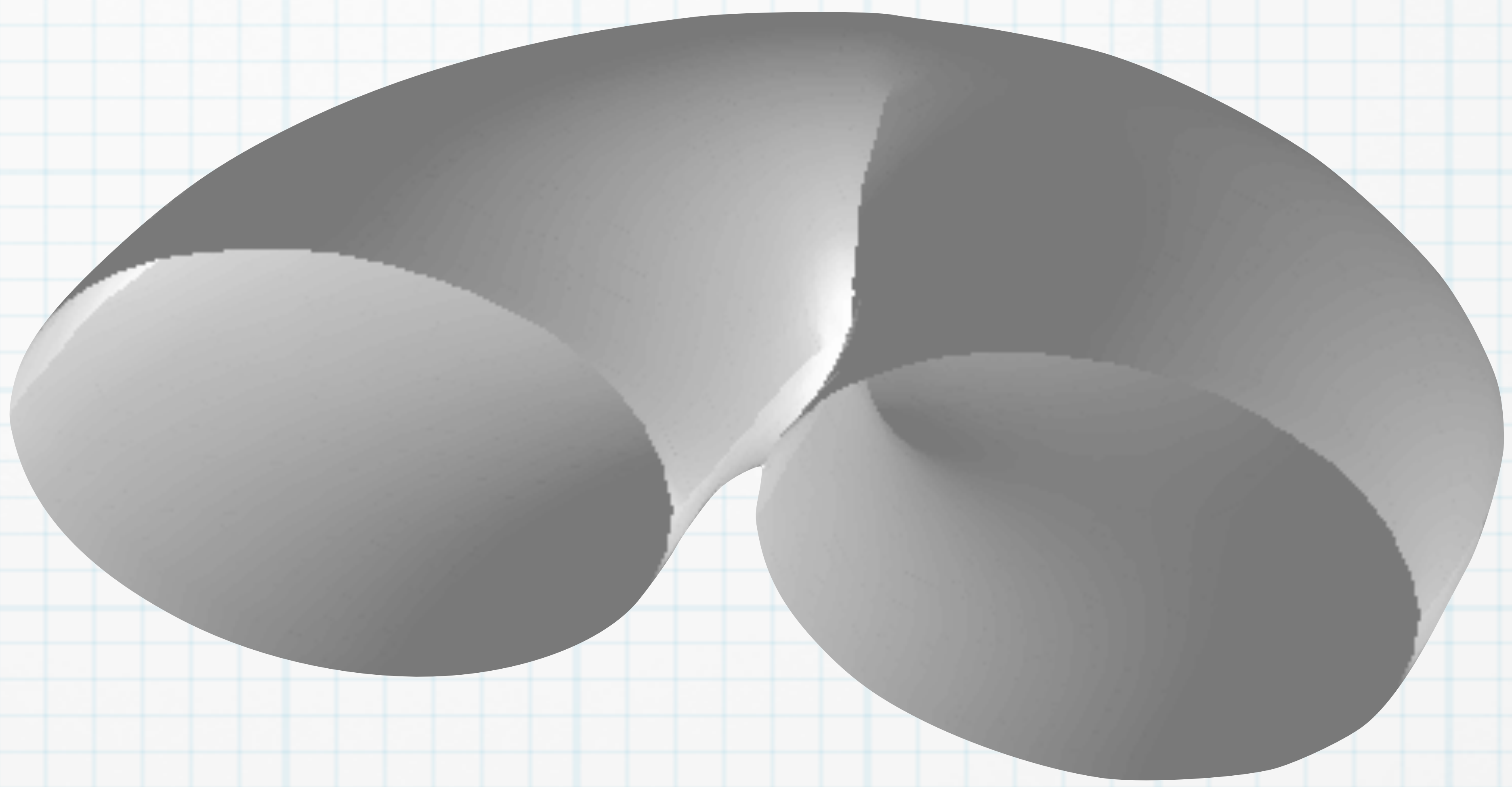
This video is also available online at http://hdl.handle.net/1813/43794

Top View – Thin Shell Opening

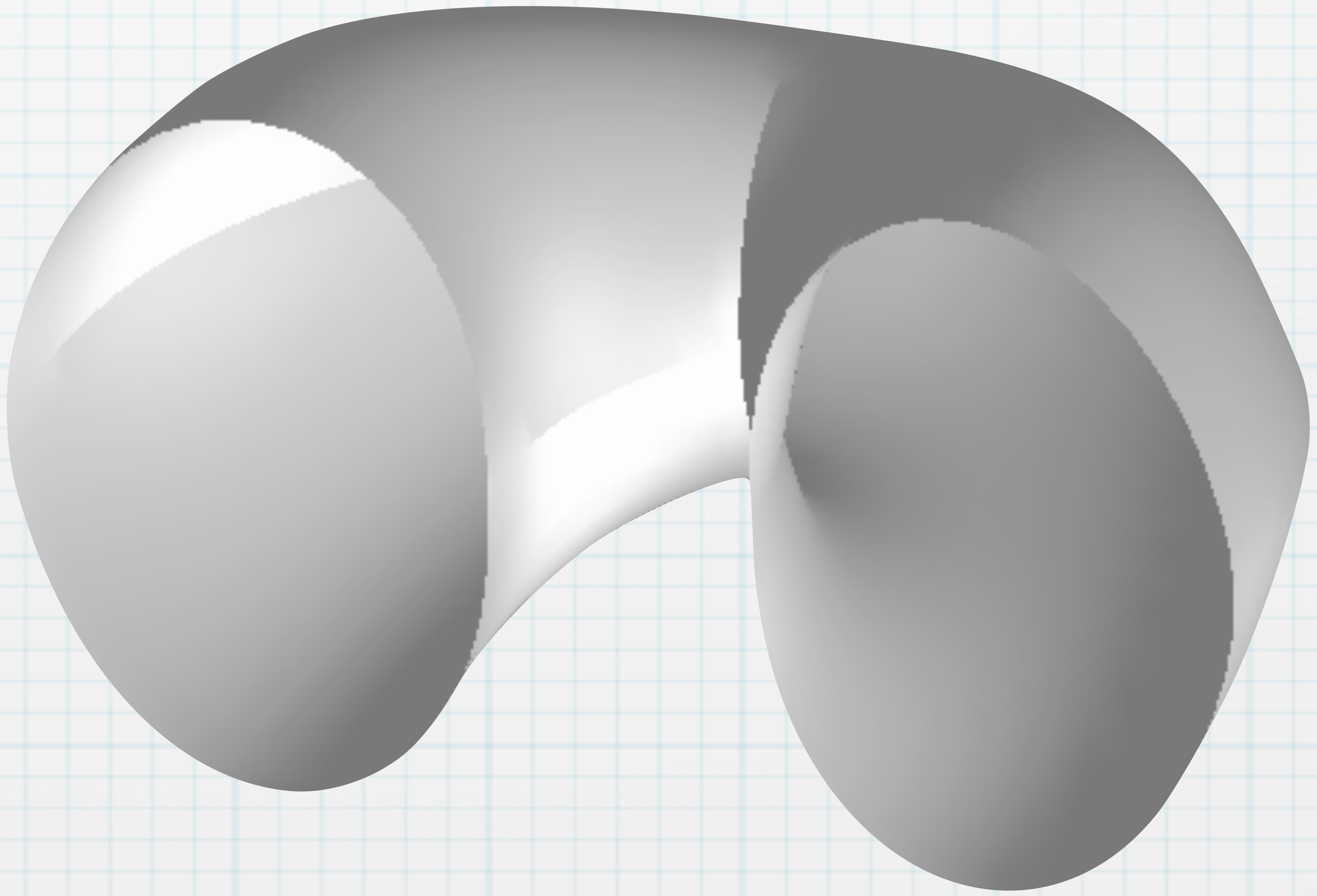


Top View – Thick Shell Opening

Shell:
Undeformed

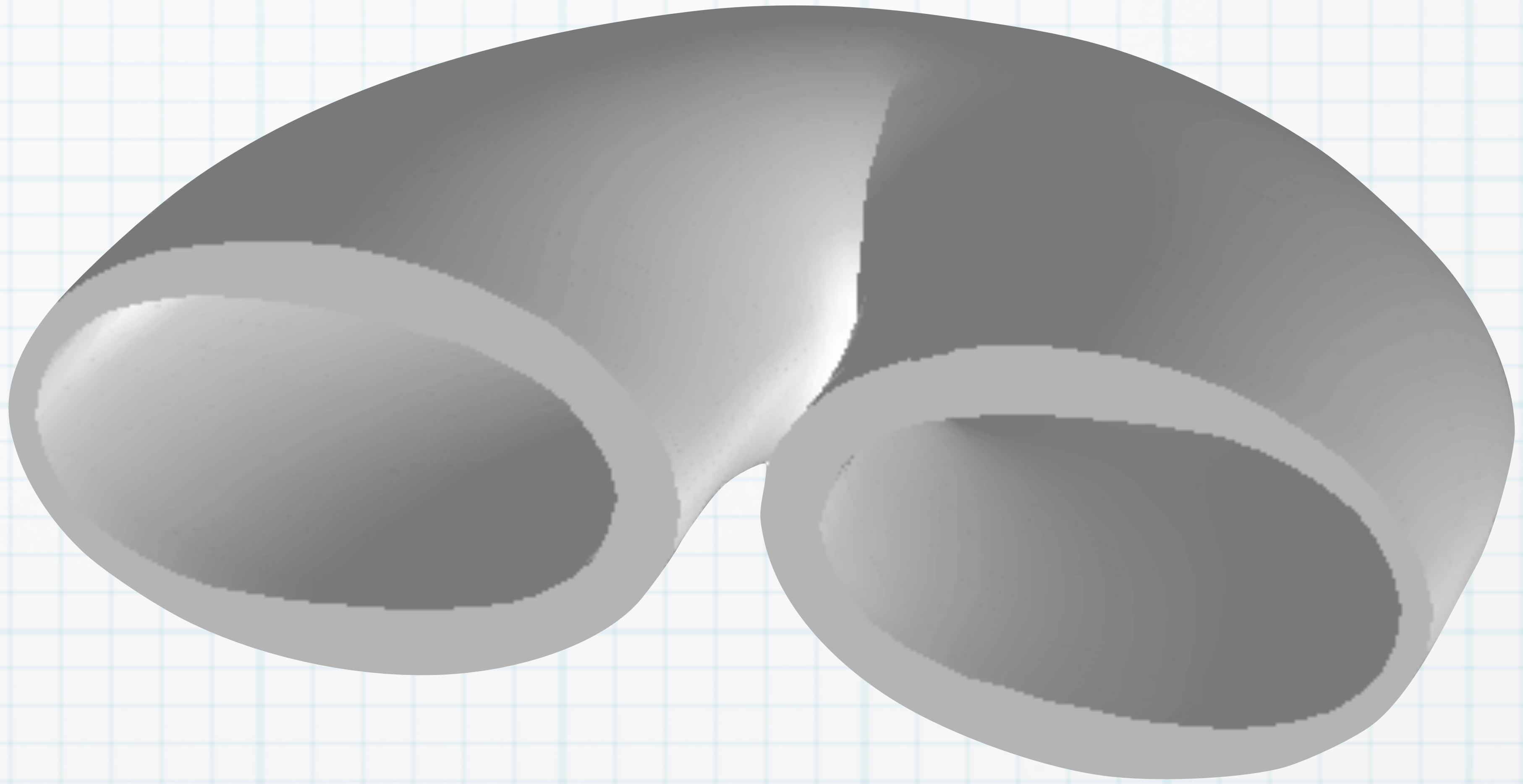


Shell:
Deformed

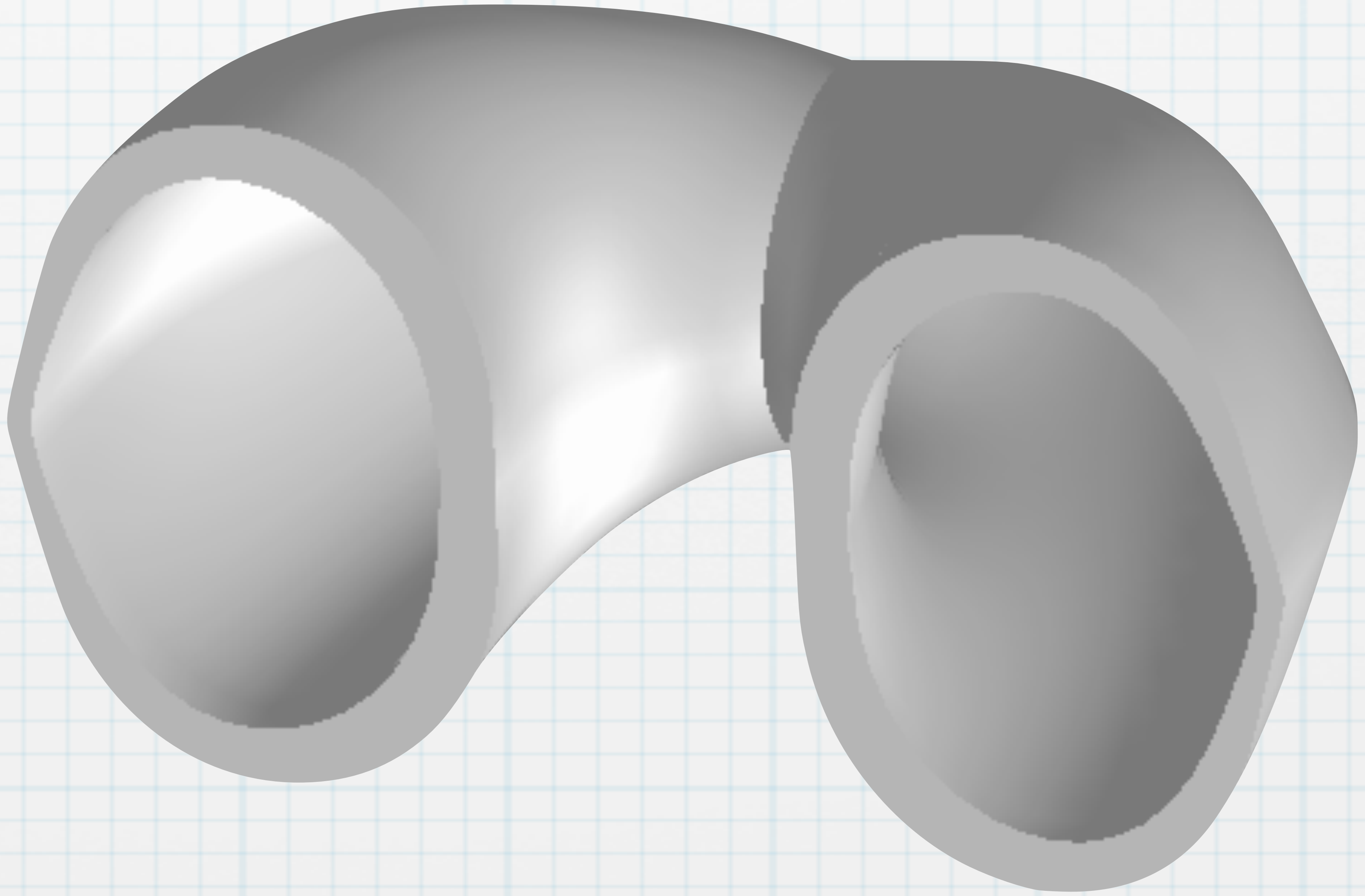


Thin and thick cell walls have similar responses.

Solid:
Undeformed



Solid:
Deformed



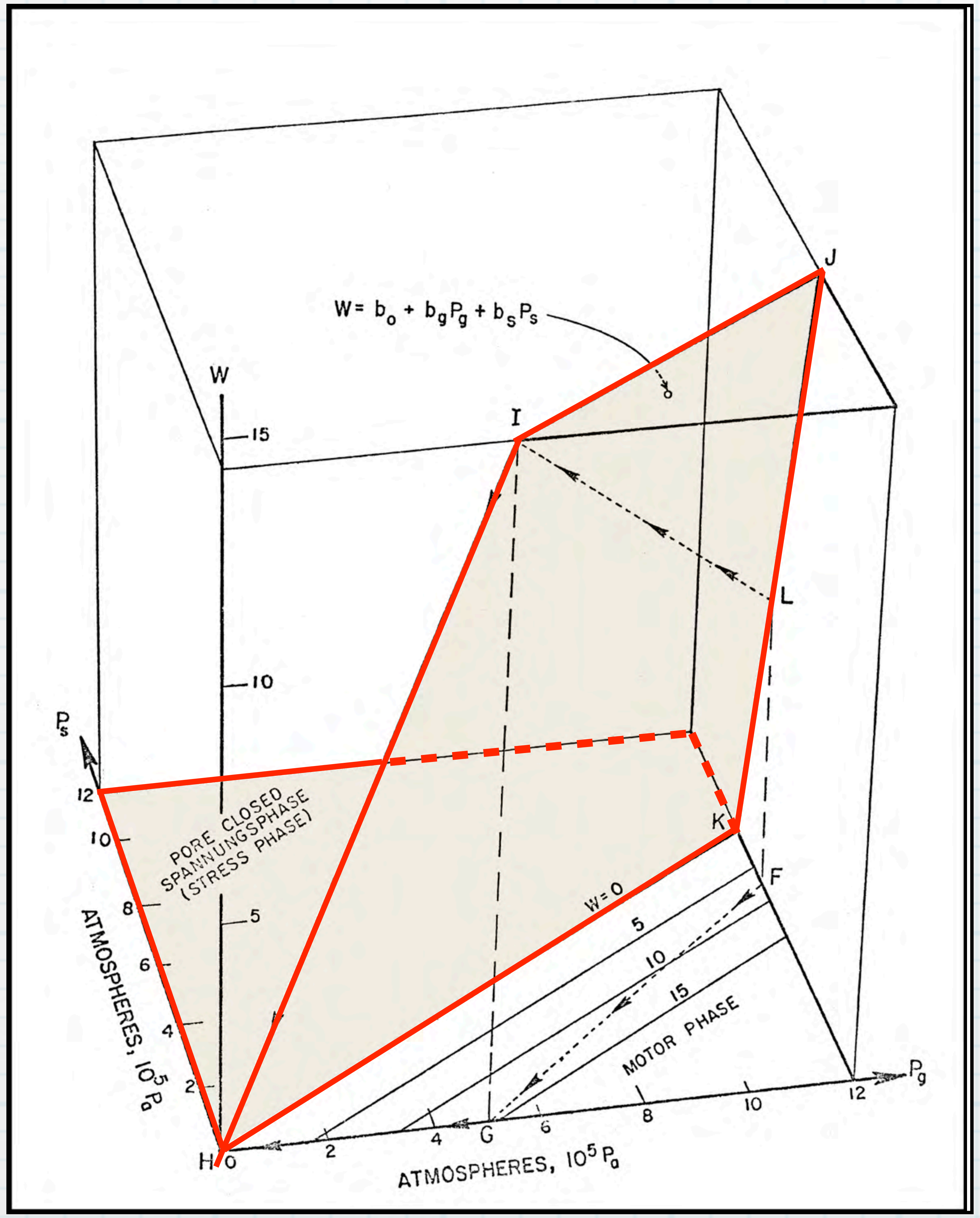
Elevation View – Thin Shell Opening

Elevation View – Thick Shell Opening

Consider the **time-dependent** opening of a pore in relation to the stomatal system.

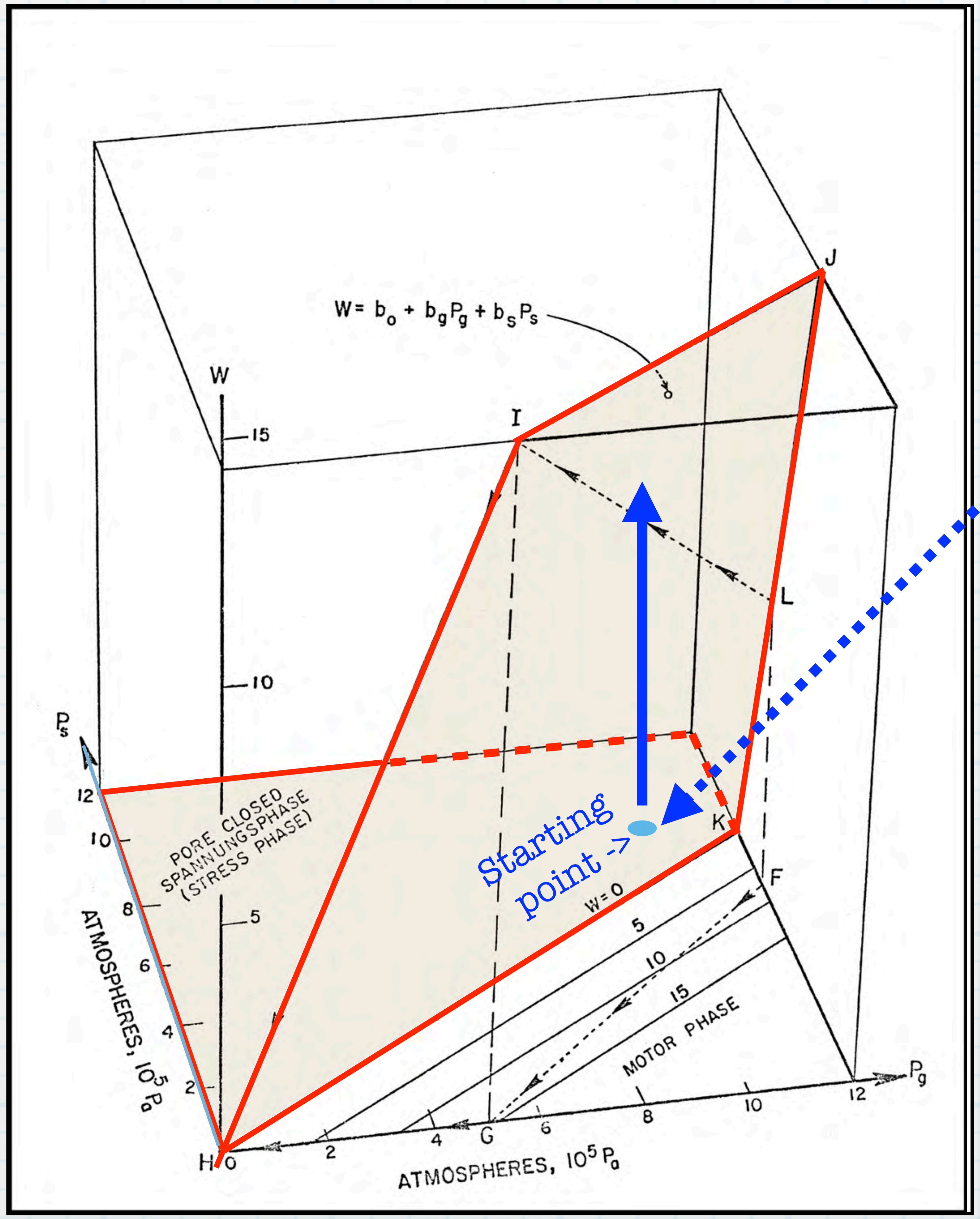
Delwiche, M.J., and J.R. Cooke. 1977. An analytical model of the hydraulic aspects of stomatal dynamics. J. Theoretical Biology 69: 113-141

Width is a function of guard cell and surrounding cell pressures



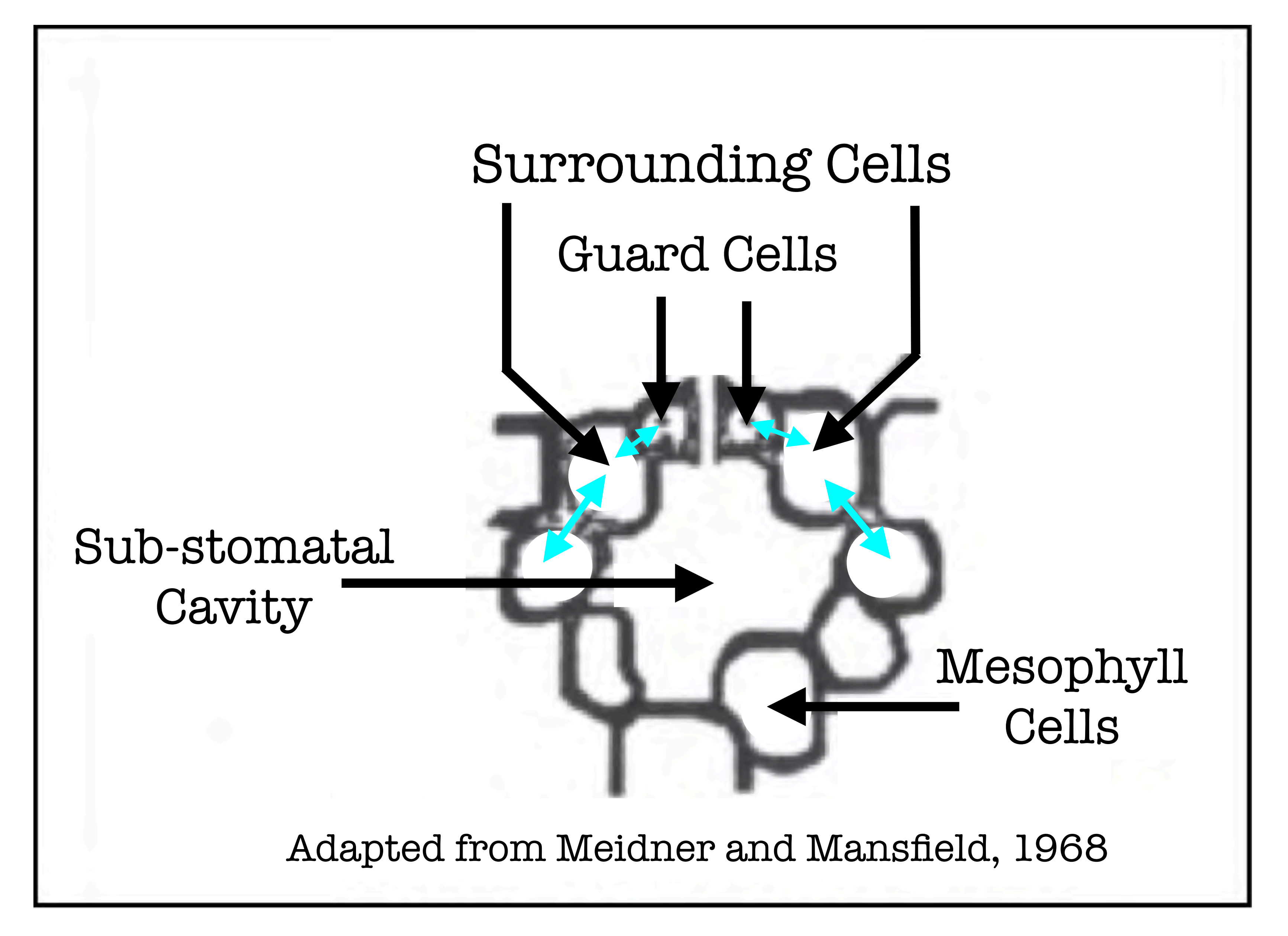
* The width surface consists of two intersecting (shaded) planes.
* Because pore width cannot be negative (more closed than closed), different equations apply to each of these shaded regions.

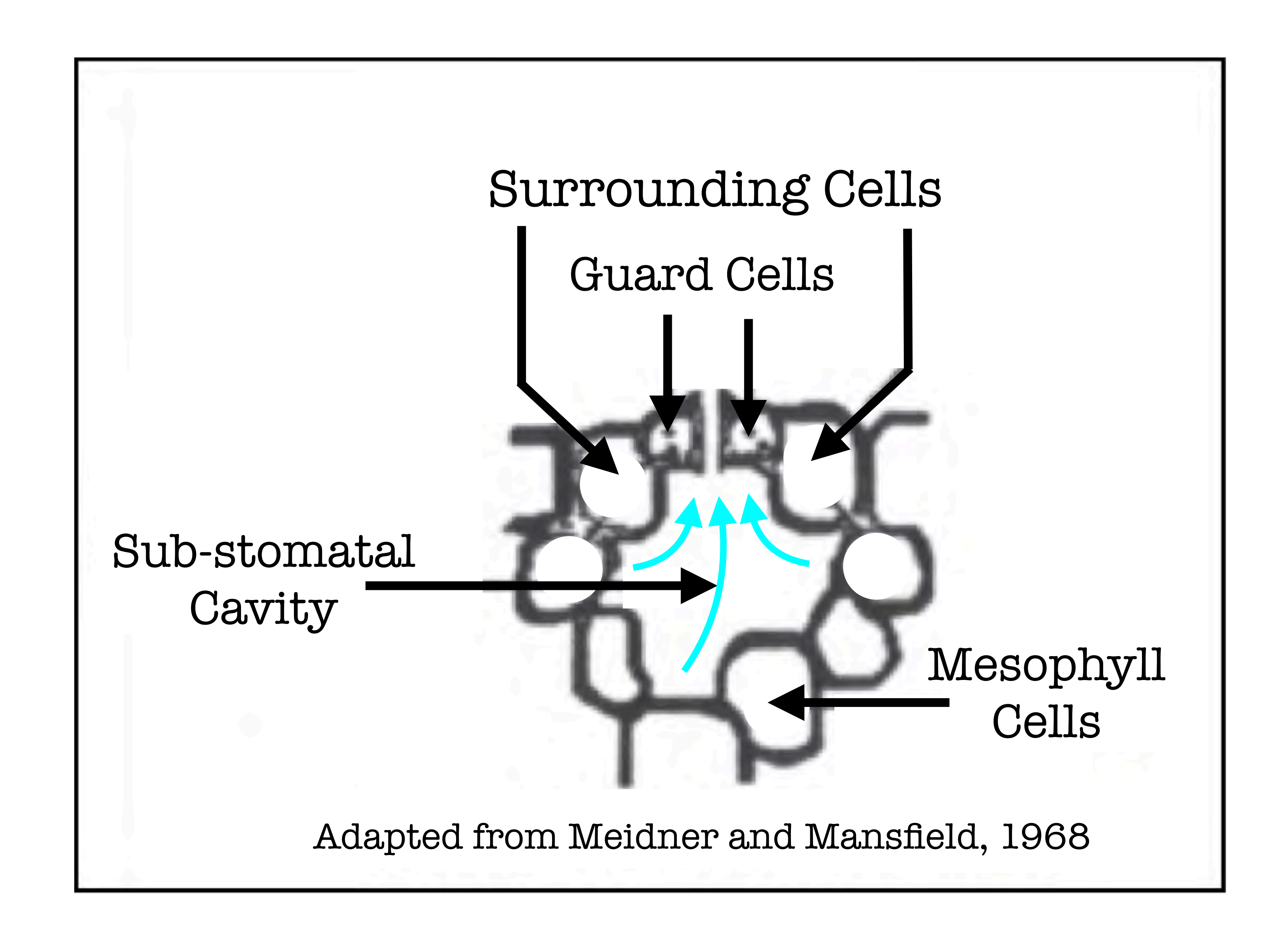
Initial conditions, i.e. starting point



* Every (Pg,Ps) pair corresponds to a point on the width surface (two intersecting, shaded planes).
* Choose a (Pg,Ps) starting point in the stress phase, i.e., width = 0).
* Assume that the osmotic potential in the guard cell is initially zero, and that sunshine on the guard cell initiates a change in its osmotic potential.

Model of the Transient Response

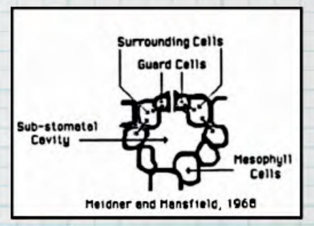




Overview of the TRANSIENT opening

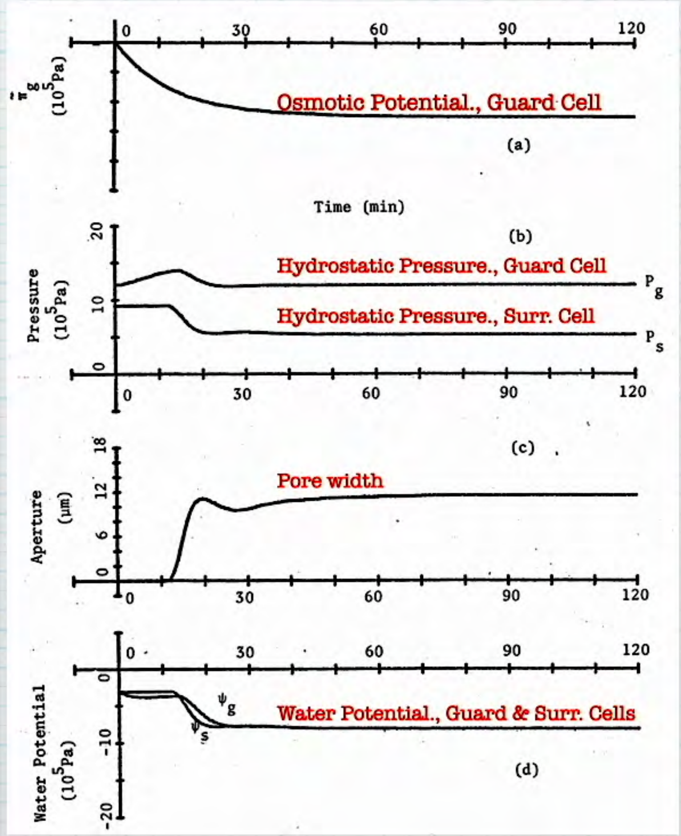
Let's now consider how the **pore width** is changed by water movement through the membranes between the cells (guard, surrounding and mesophyll) and by the associated diffusion from the sub-stomatal cavity into the environment.

Transient pore opening



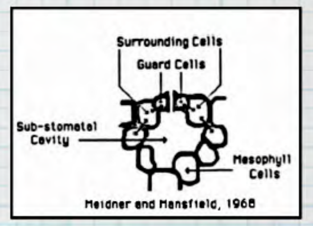
The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:



[1]

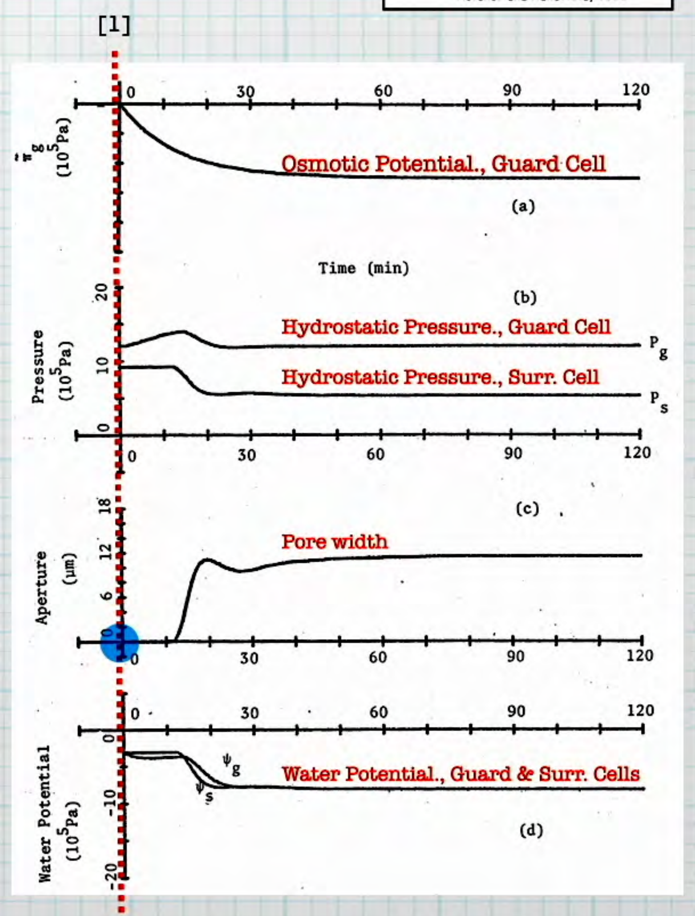
Transient pore opening



The four (4) graphs at right share a common time axis.

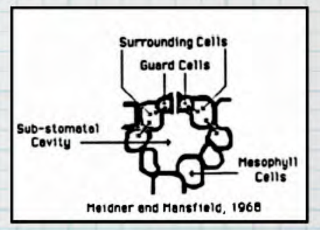
Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0



[2]

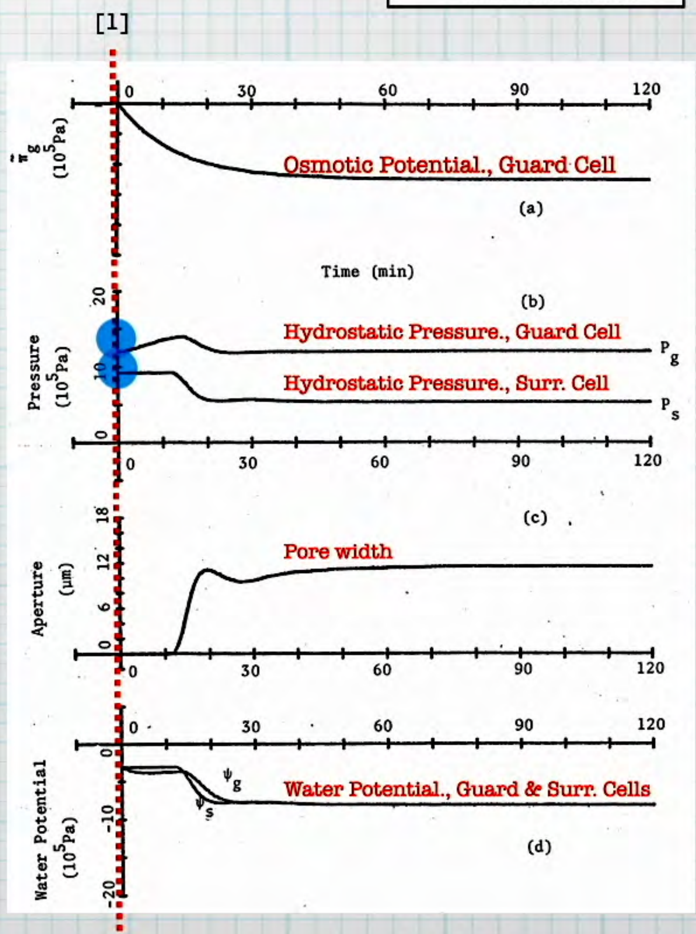
Transient pore opening



The four (4) graphs at right share a common time axis.

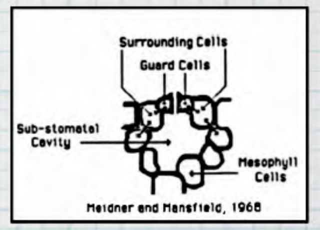
Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0
  - Pg and Ps in the stress phase



[3]

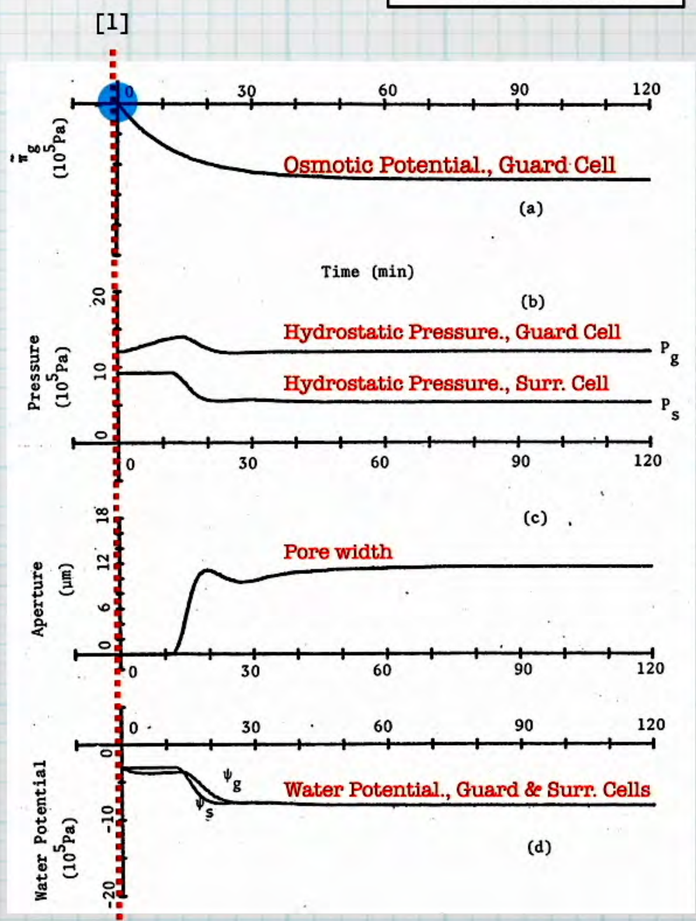
Transient pore opening



The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0
  - Pg and Ps in the stress phase
  - osmotic potential in the guard cell is zero.



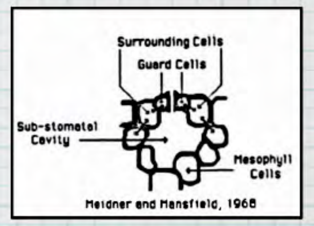
[4]

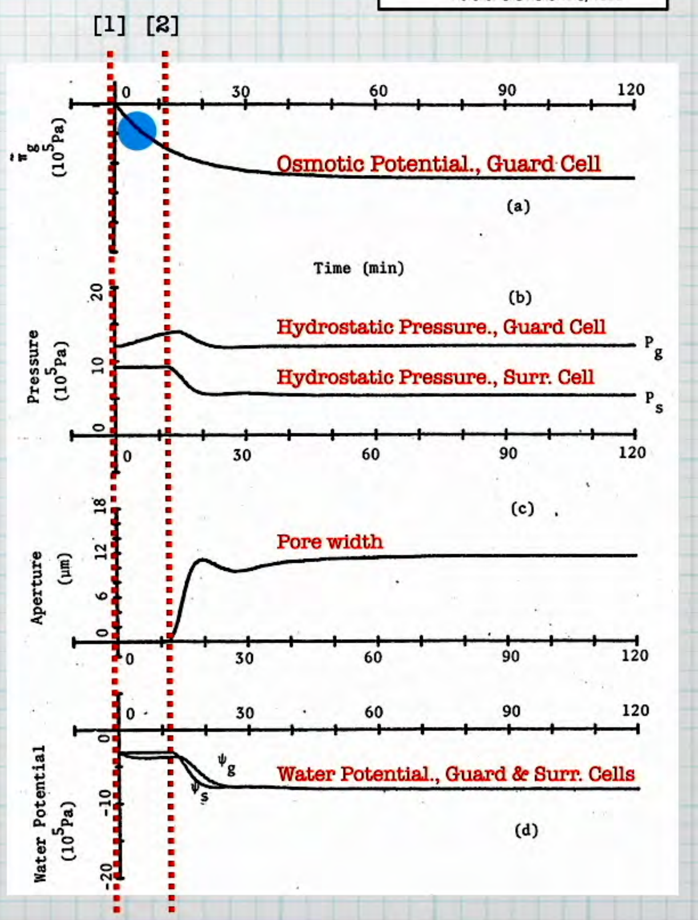
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0
  - Pg and Ps in the stress phase
  - osmotic potential in the guard cell is zero.
- 2. Suppose that the osmotic potential in the guard cell drops.





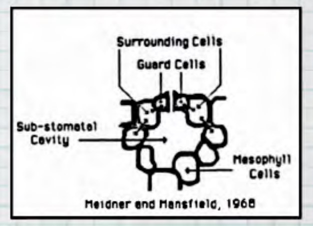
[5]

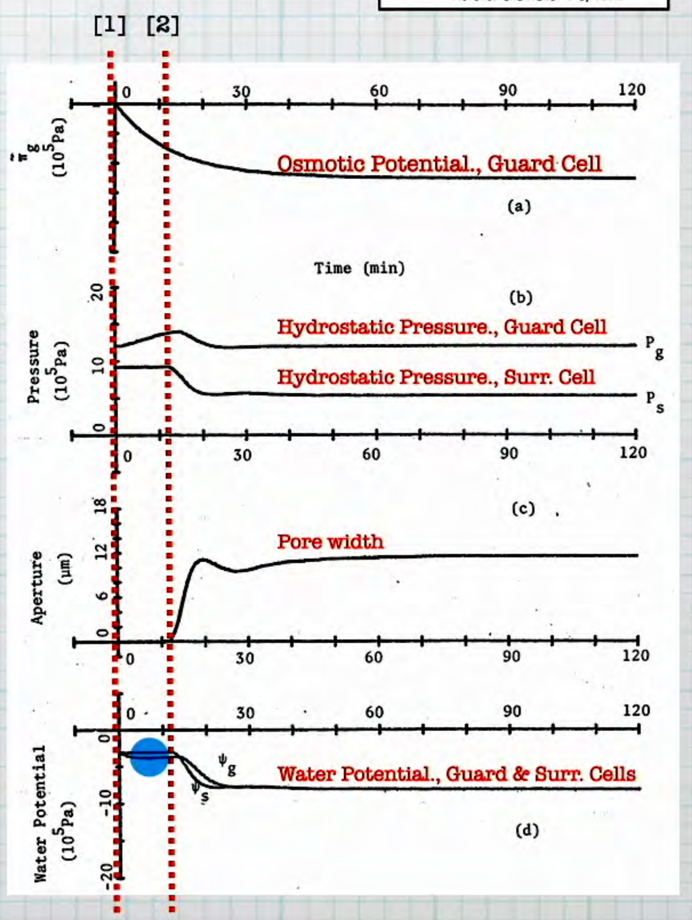
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0
  - Pg and Ps in the stress phase
  - osmotic potential in the guard cell is zero.
- 2. Suppose that the osmotic potential in the guard cell drops.
  - This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.





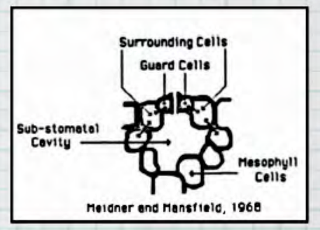
[6]

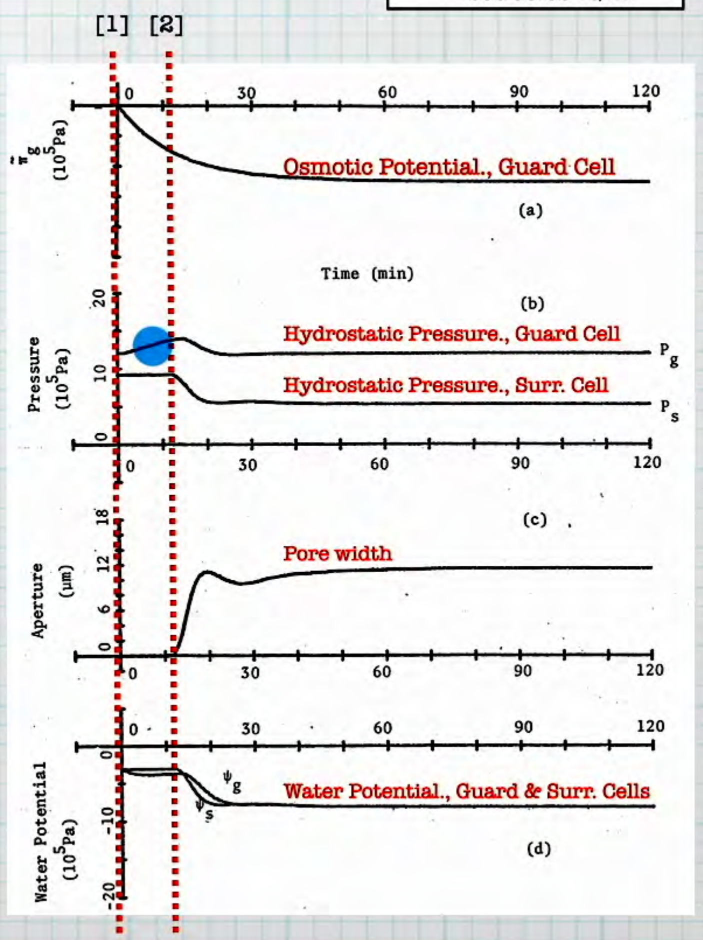
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0
  - Pg and Ps in the stress phase
  - osmotic potential in the guard cell is zero.
- 2. Suppose that the osmotic potential in the guard cell drops.
  - This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  - This influx of water increases the guard cell pressure.





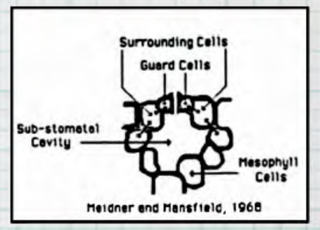
[7]

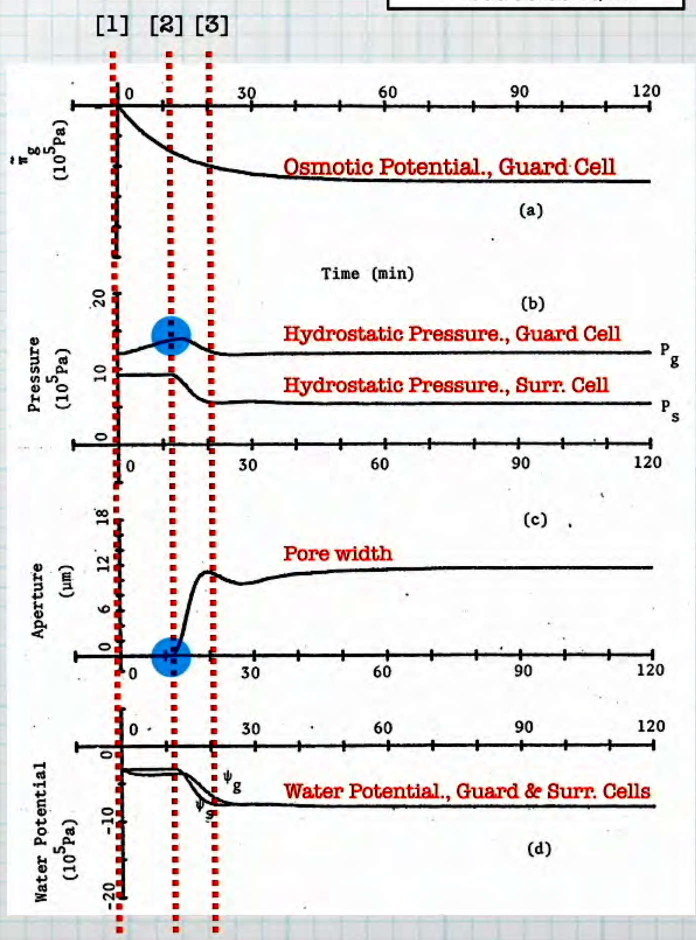
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

- 1. Initial conditions (at time=0):
  - width = 0
  - Pg and Ps in the stress phase
  - osmotic potential in the guard cell is zero.
- 2. Suppose that the osmotic potential in the guard cell drops.
  - This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  - This influx of water increases the guard cell pressure.
  - Eventually the guard cell pressure increases enough to initiate pore opening.





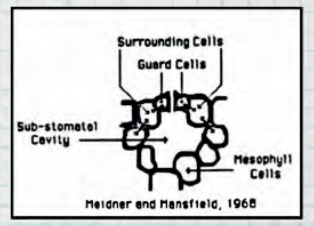
[8]

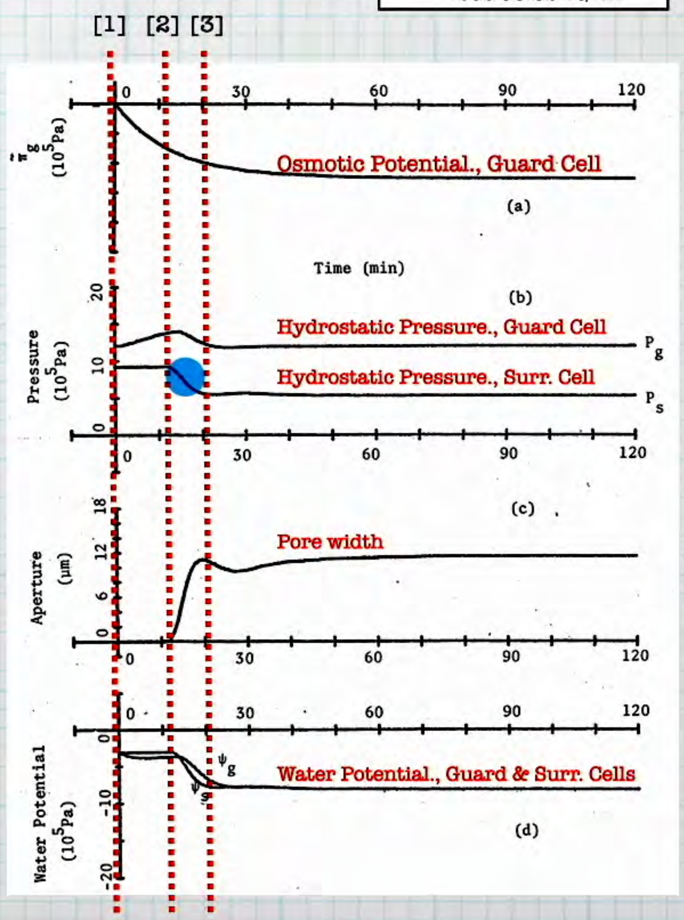
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

* 1. Initial conditions (at time=0):
  * width = 0
  * Pg and Ps in the stress phase
  * osmotic potential in the guard cell is zero.
* 2. Suppose that the osmotic potential in the guard cell drops.
  * This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  * This influx of water increases the guard cell pressure.
  * Eventually the guard cell pressure increases enough to initiate pore opening.
* 3. Water diffuses through the open pore into the environment, thereby decreasing the surrounding cell pressure.





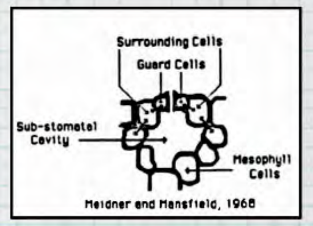
[9]

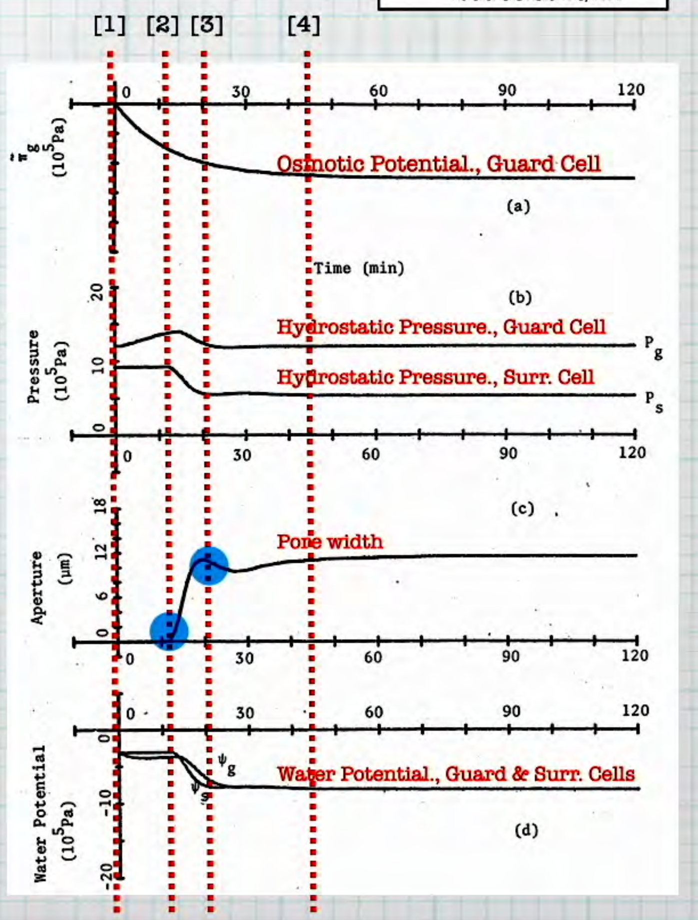
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

* 1. Initial conditions (at time=0):
  * width = 0
  * Pg and Ps in the stress phase
  * osmotic potential in the guard cell is zero.
* 2. Suppose that the osmotic potential in the guard cell drops.
  * This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  * This influx of water increases the guard cell pressure.
  * Eventually the guard cell pressure increases enough to initiate pore opening.
* 3. Water diffuses through the open pore into the environment, thereby decreasing the surrounding cell pressure.
  * The pore "pops" open.





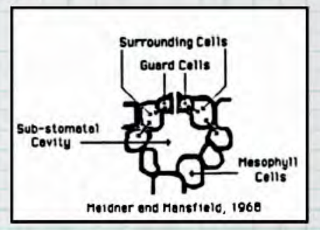
[10]

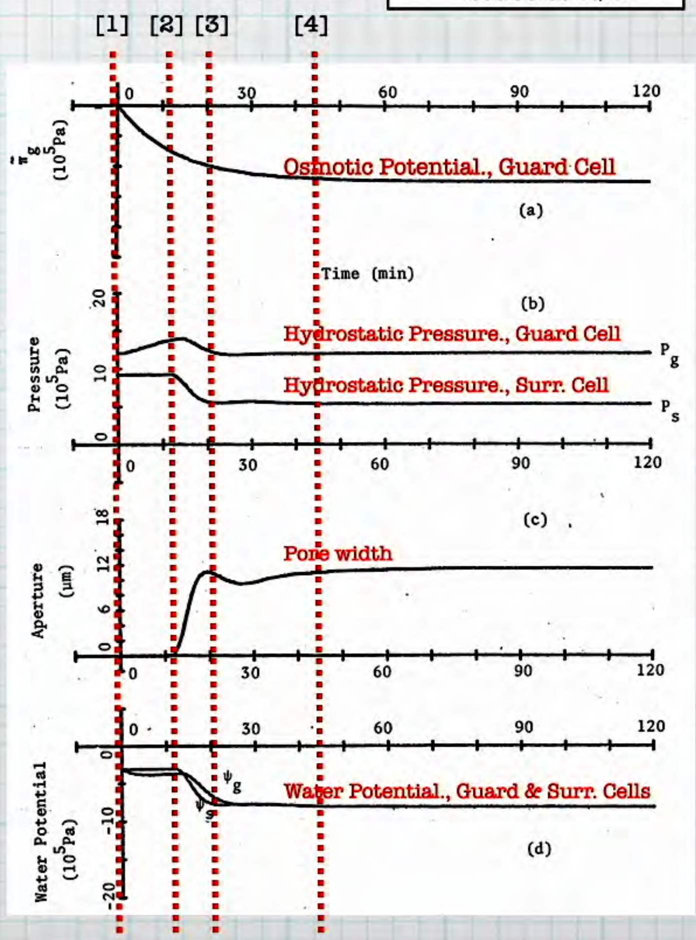
Transient pore opening

The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

* 1. Initial conditions (at time=0):
  * width = 0
  * Pg and Ps in the stress phase
  * osmotic potential in the guard cell is zero.
* 2. Suppose that the osmotic potential in the guard cell drops.
  * This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  * This influx of water increases the guard cell pressure.
  * Eventually the guard cell pressure increases enough to initiate pore opening.
* 3. Water diffuses through the open pore into the environment, thereby decreasing the surrounding cell pressure.
  * The pore "pops" open.
  * The increasing guard cell pressure triggered the opening, but the drop in surrounding cell pressure accounts for the rapid opening of the pore.





[11]

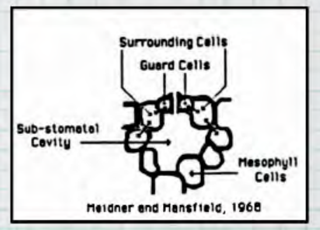
Transient pore opening

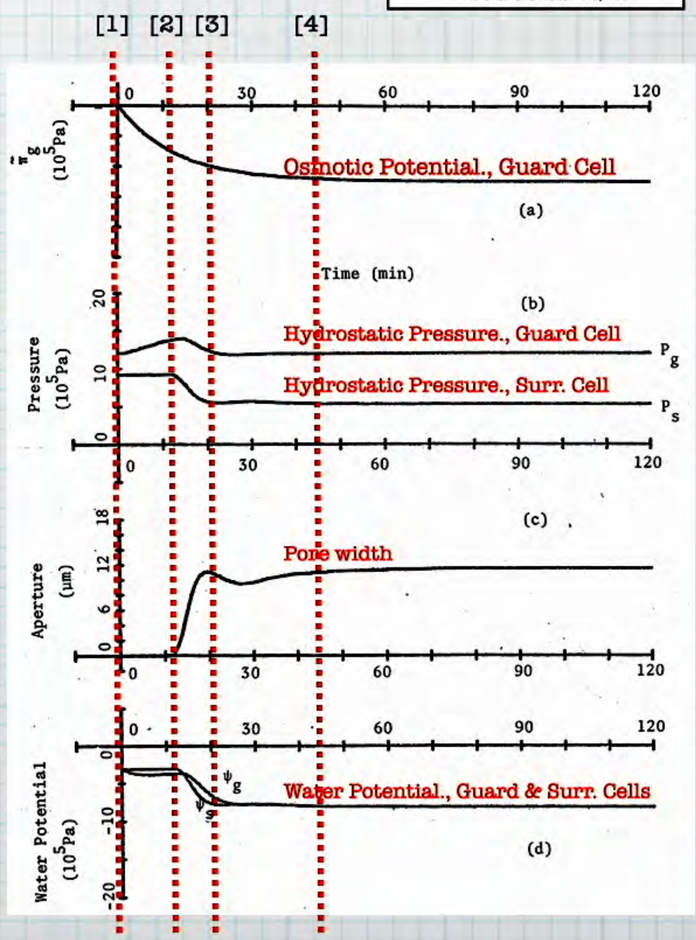
The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

* 1. Initial conditions (at time=0):
  * width = 0
  * Pg and Ps in the stress phase
  * osmotic potential in the guard cell is zero.
* 2. Suppose that the osmotic potential in the guard cell drops.
  * This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  * This influx of water increases the guard cell pressure.
  * Eventually the guard cell pressure increases enough to initiate pore opening.
* 3. Water diffuses through the open pore into the environment, thereby decreasing the surrounding cell pressure.
  * The pore "pops" open.
  * The increasing guard cell pressure triggered the opening, but the drop in surrounding cell pressure accounts for the rapid opening of the pore.

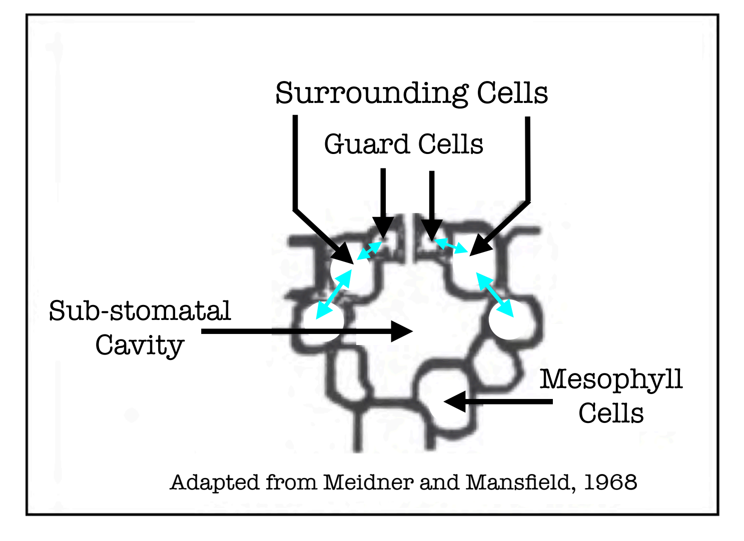
This opening is a passive response; active transport had not yet been incorporated into the model at this point.





[12]

Transient pore opening

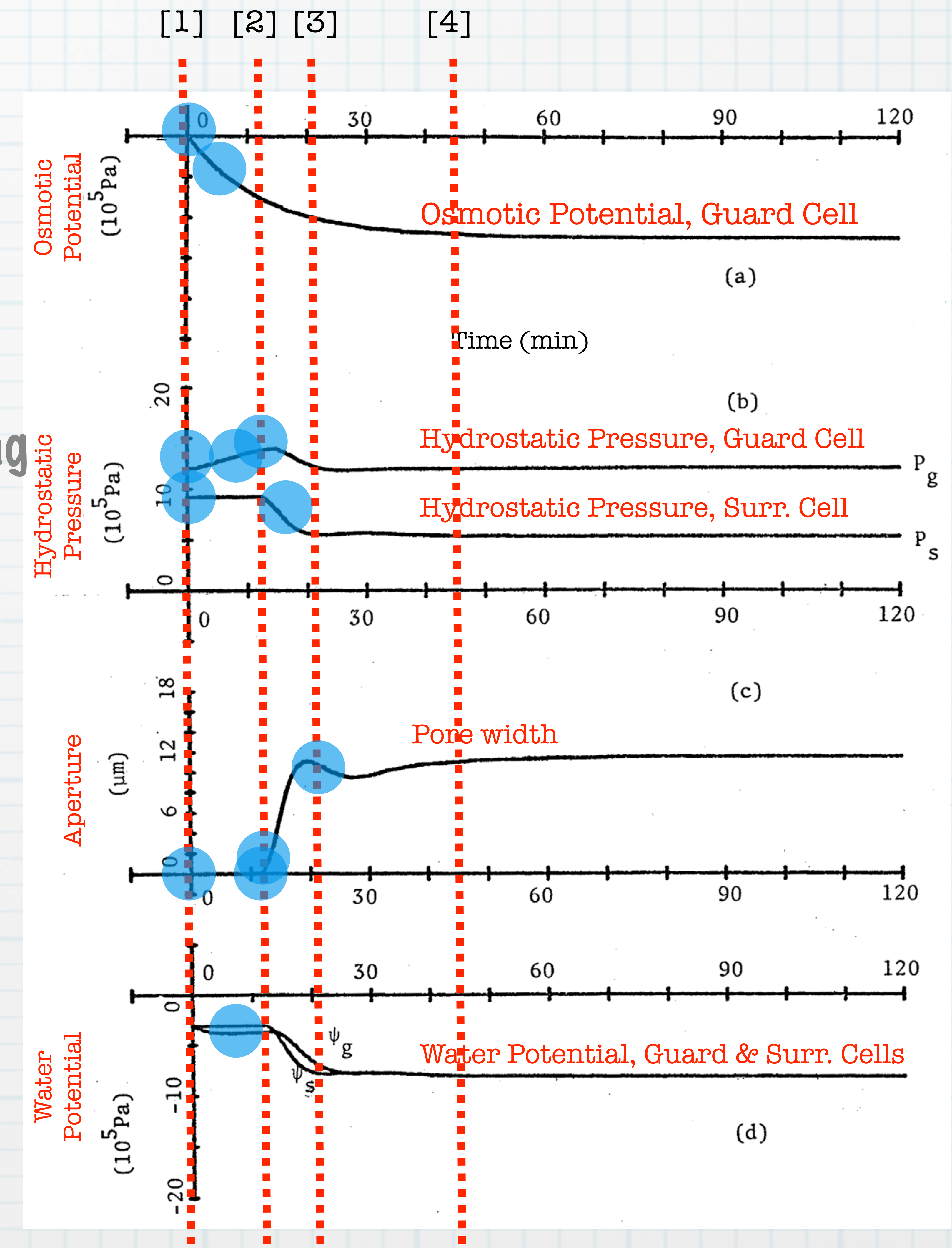


The four (4) graphs at right share a common time axis.

Here's a pore opening scenario:

* 1. Initial conditions (at time=0):
  * width = 0
  * Pg and Ps in the stress phase
  * osmotic potential in the guard cell is zero.
* 2. Suppose that the osmotic potential in the guard cell drops.
  * This water potential difference created between guard cell and surrounding cell causes water to move into the guard cell from the surrounding cell.
  * This influx of water increases the guard cell pressure.
  * Eventually the guard cell pressure increases enough to initiate pore opening.
* 3. Water diffuses through the open pore into the environment, thereby decreasing the surrounding cell pressure.
  * The pore "pops" open.
  * The increasing guard cell pressure triggered the opening, but the drop in surrounding cell pressure accounts for the rapid opening of the pore.

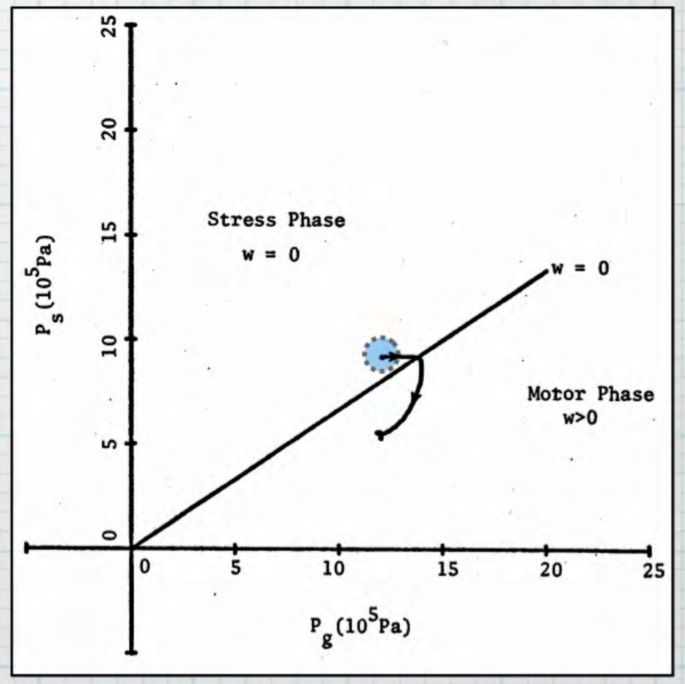
This opening is a passive response; active transport had not yet been incorporated into the model at this point.



Transient pore opening

(an alternative plot)

* Here's a Pg-Ps phase plane plot of the transient just discussed. Time = 0 starts here.

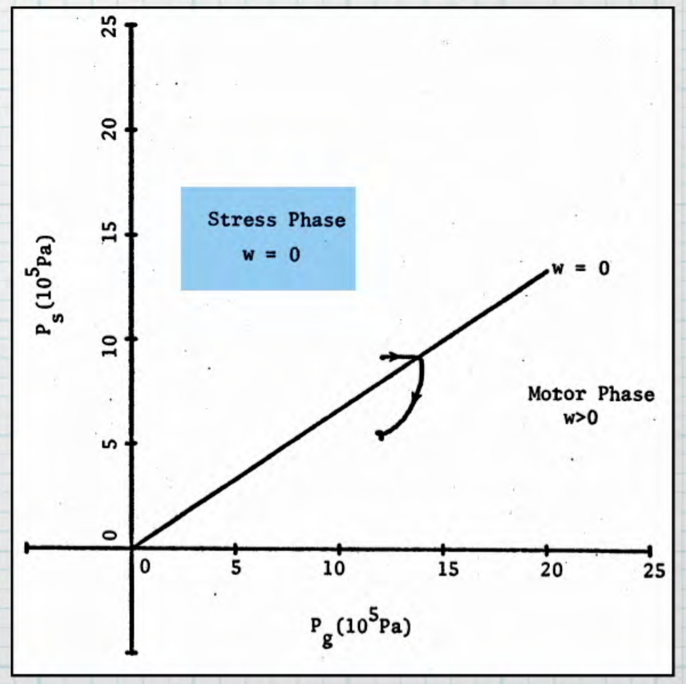


[1]

Transient pore opening

(an alternative plot)

* Here's a Pg-Ps phase plane plot of the transient just discussed. Time = 0 starts here.
* 1. Begin with a (Pg-Ps) starting point in the stress phase, i.e., the pore is closed.

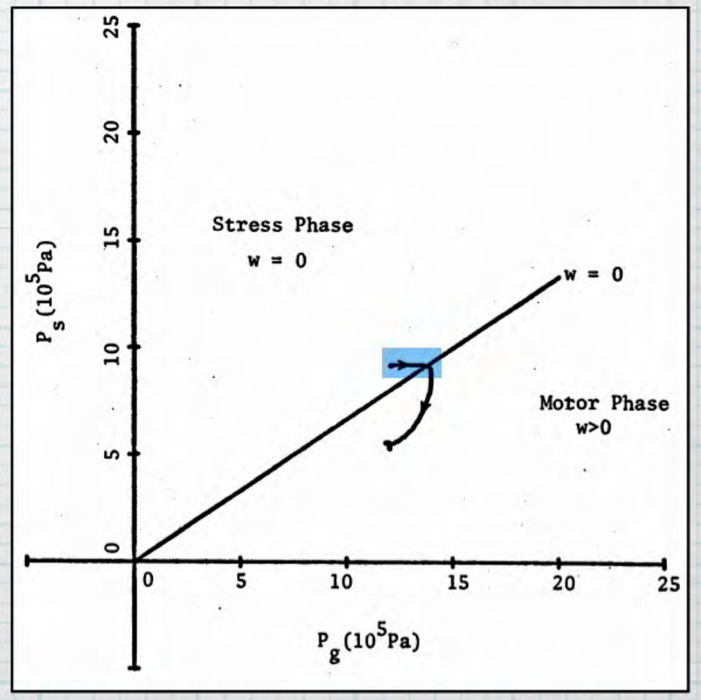


[2]

Transient pore opening

(an alternative plot)

* Here's a Pg-Ps phase plane plot of the transient just discussed. Time = 0 starts here.
* 1. Begin with a (Pg-Ps) starting point in the stress phase, i.e., the pore is closed.
* 2. Guard cell pressure Pg increases, but the surrounding cell pressure remains relatively constant.

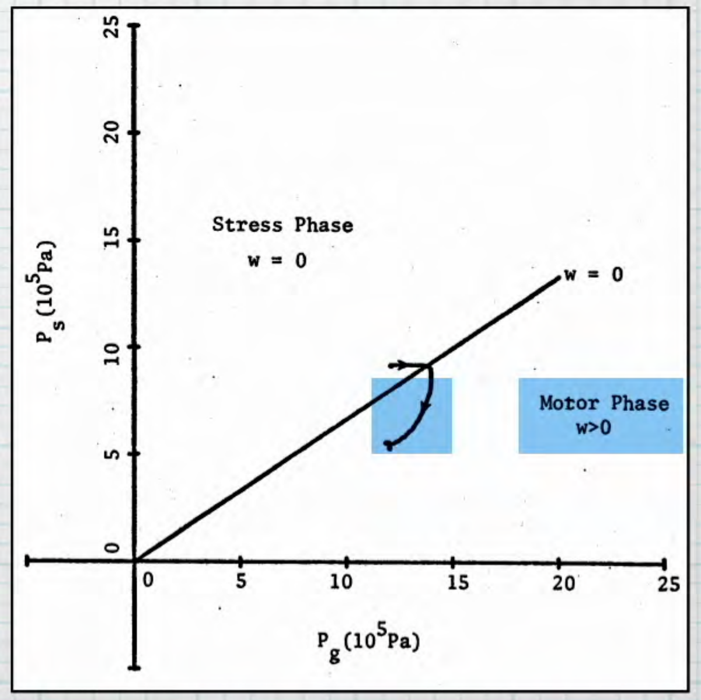


[3]

Transient pore opening

(an alternative plot)

* Here's a Pg-Ps phase plane plot of the transient just discussed. Time = 0 starts here.
* 1. Begin with a (Pg-Ps) starting point in the stress phase, i.e., the pore is closed.
* 2. Guard cell pressure Pg increases, but the surrounding cell pressure remains relatively constant.
* 3. When the pore opens, water evaporates from the cavity, dropping the surrounding cell pressure, Ps.

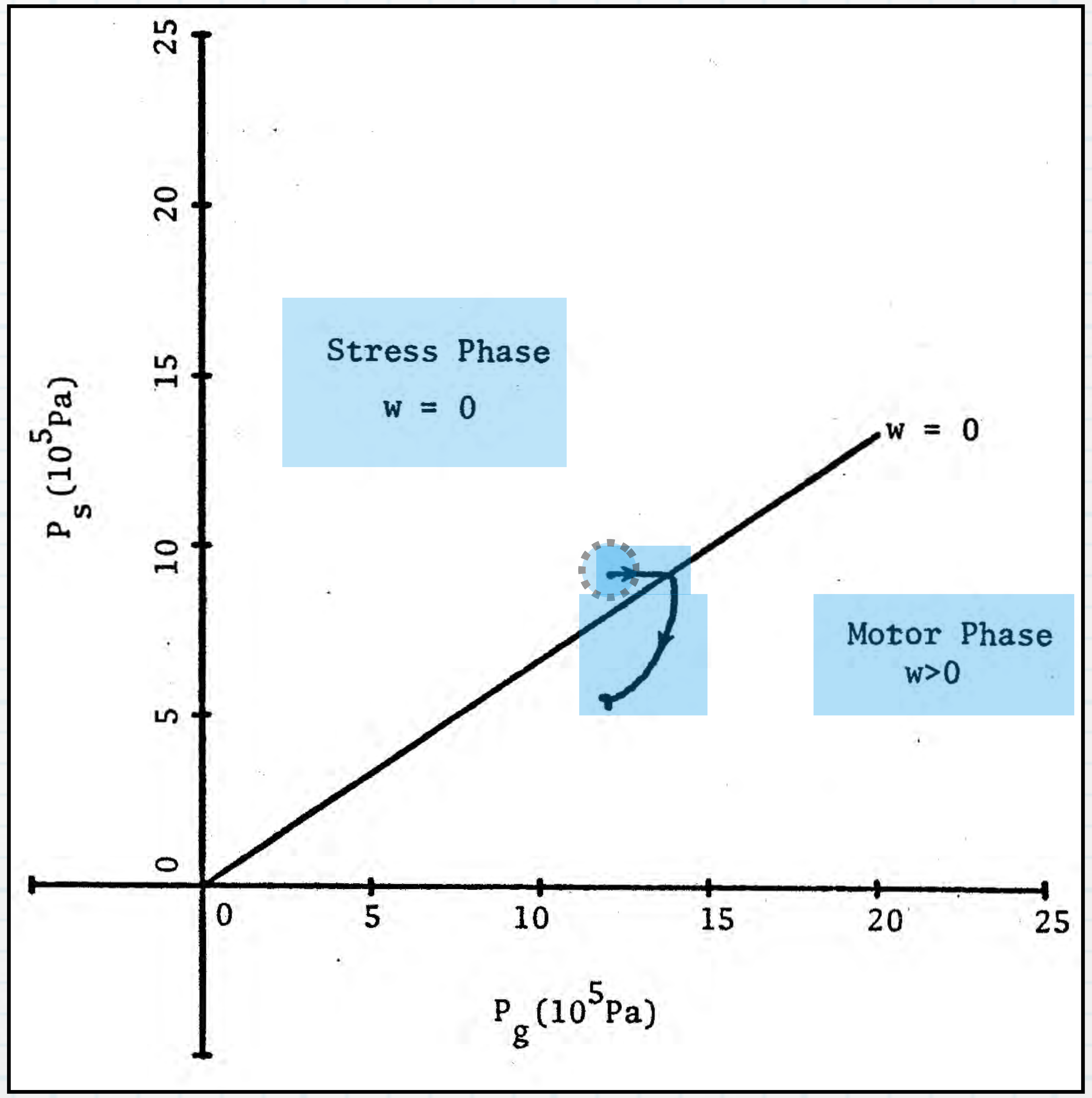


[4]

Transient pore opening

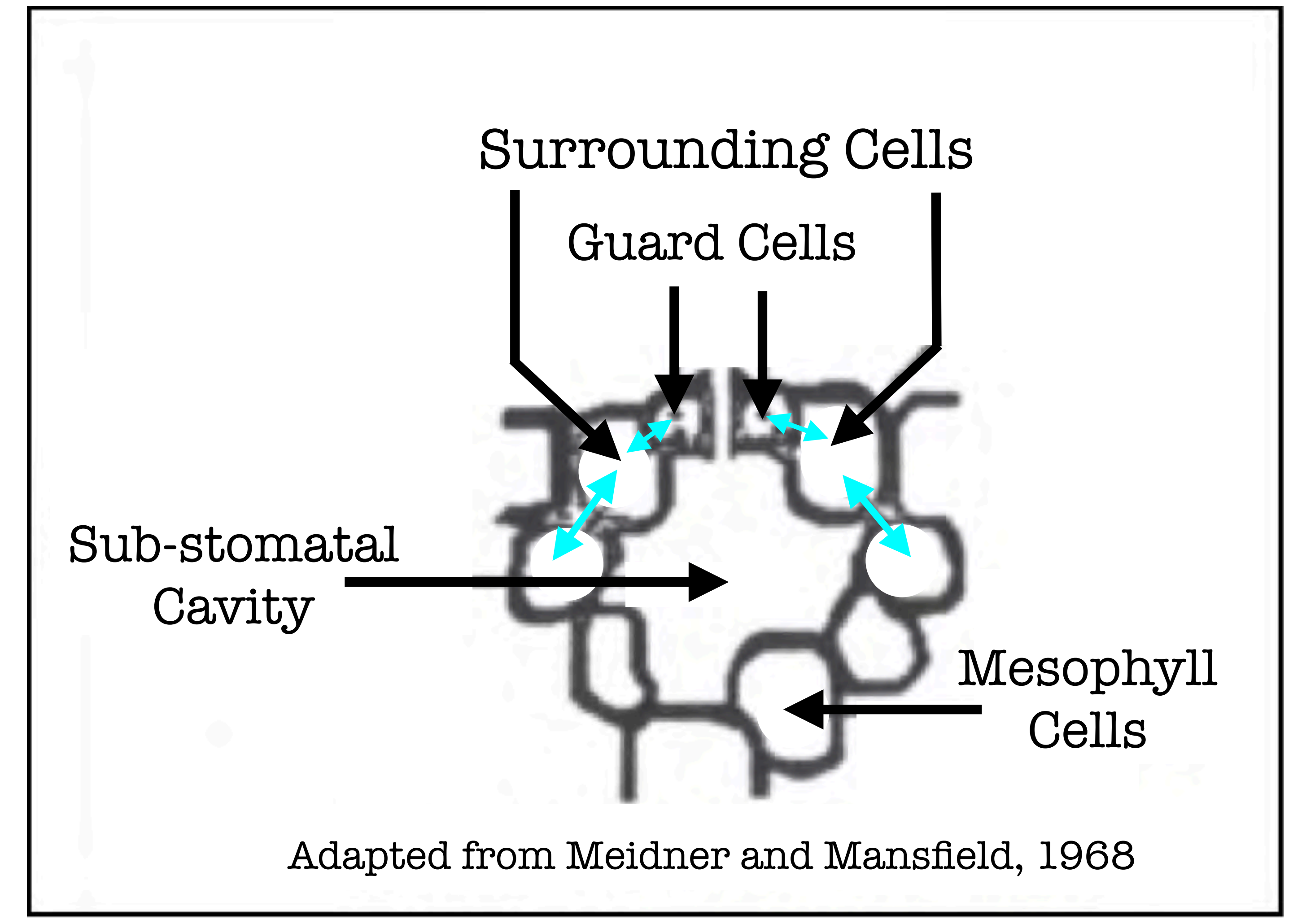
(an alternative plot)

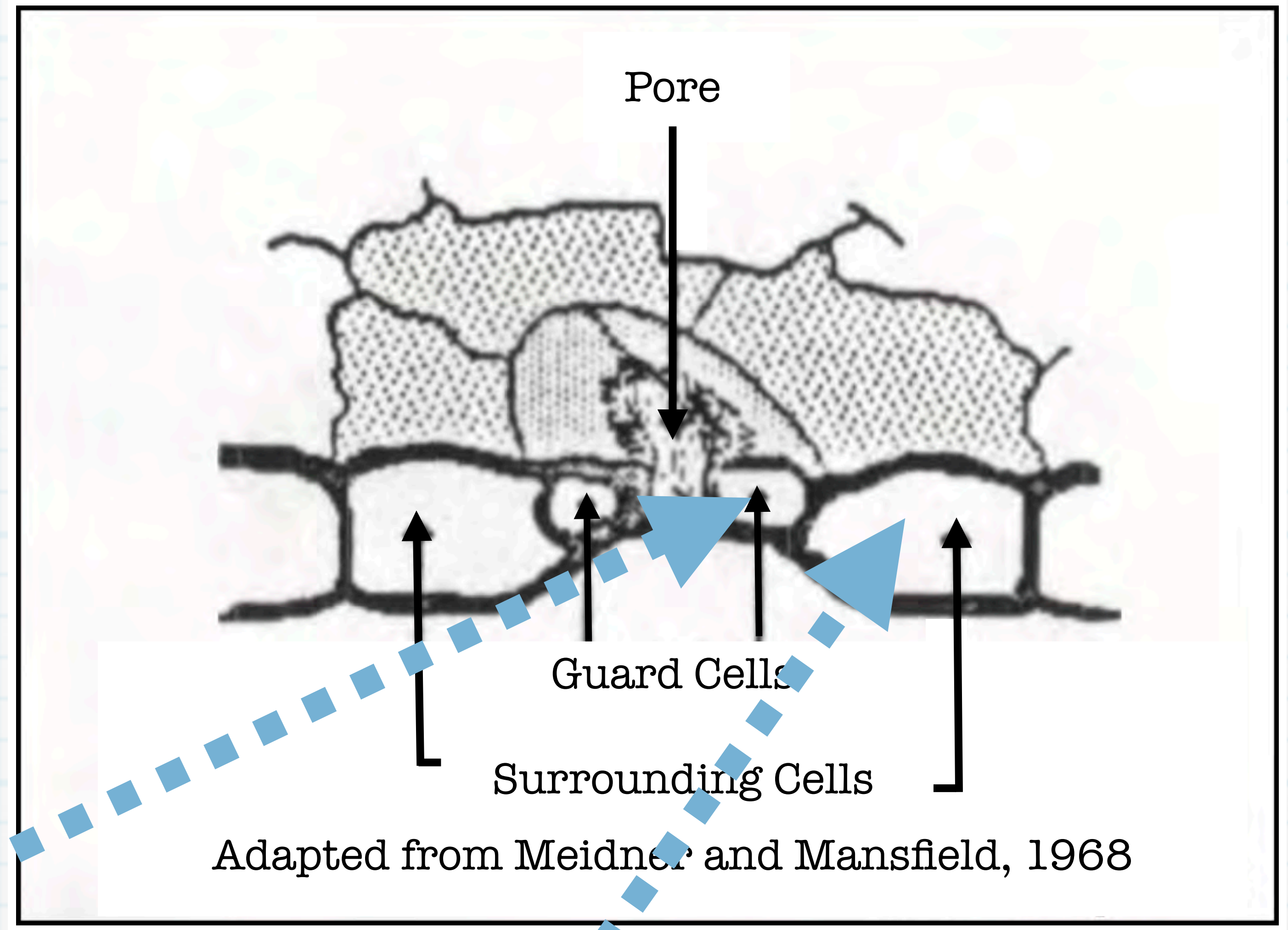
* Here's a Pg-Ps phase plane plot of the transient just discussed. Time = 0 starts here.
* 1. Begin with a (Pg-Ps) starting point in the stress phase, i.e., the pore is closed.
* 2. Guard cell pressure Pg increases, but the surrounding cell pressure remains relatively constant.
* 3. When the pore opens, water evaporates from the cavity, dropping the surrounding cell pressure, Ps.



* 4. The reduction in the restraining force (the surrounding cell pressure Ps) accounts for the rapid opening of the pore.

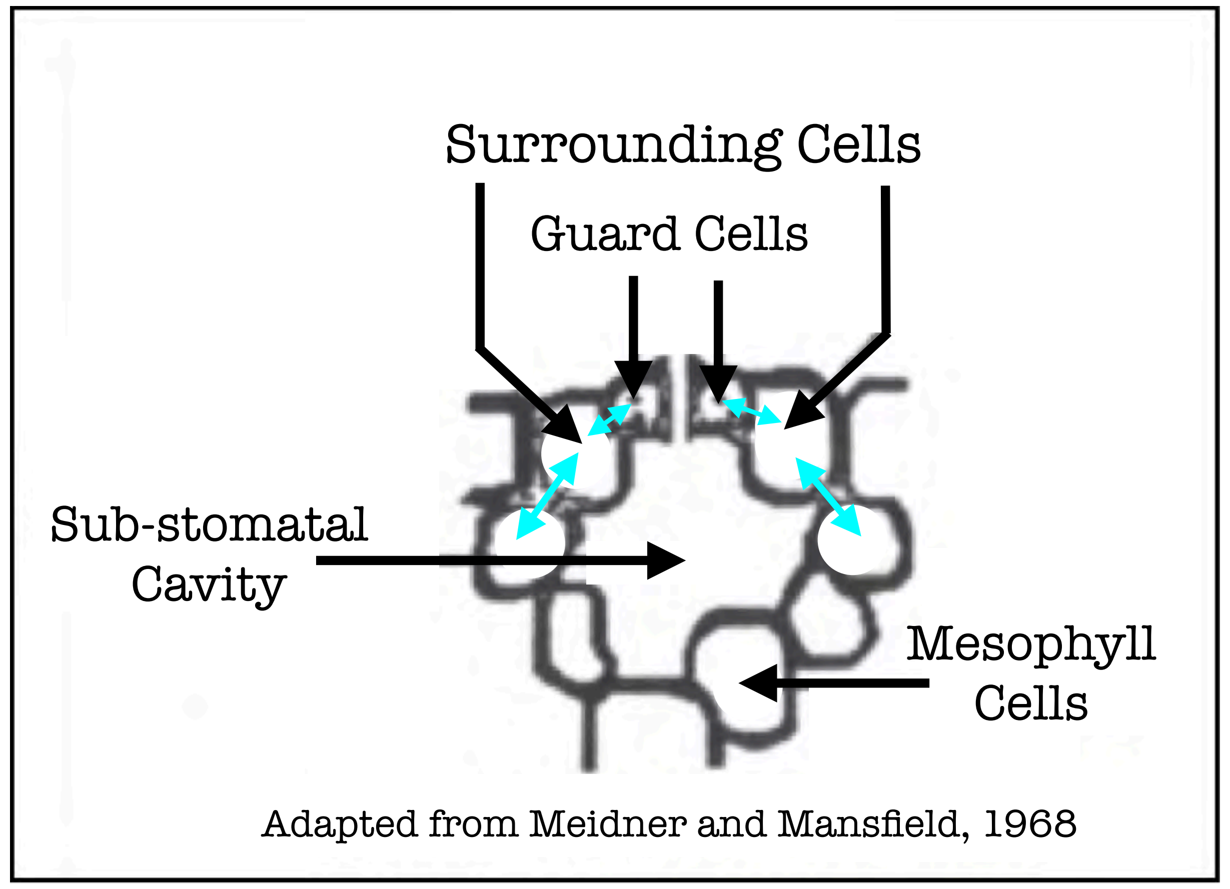
Importance of micelle for time-dependent conditions (1)

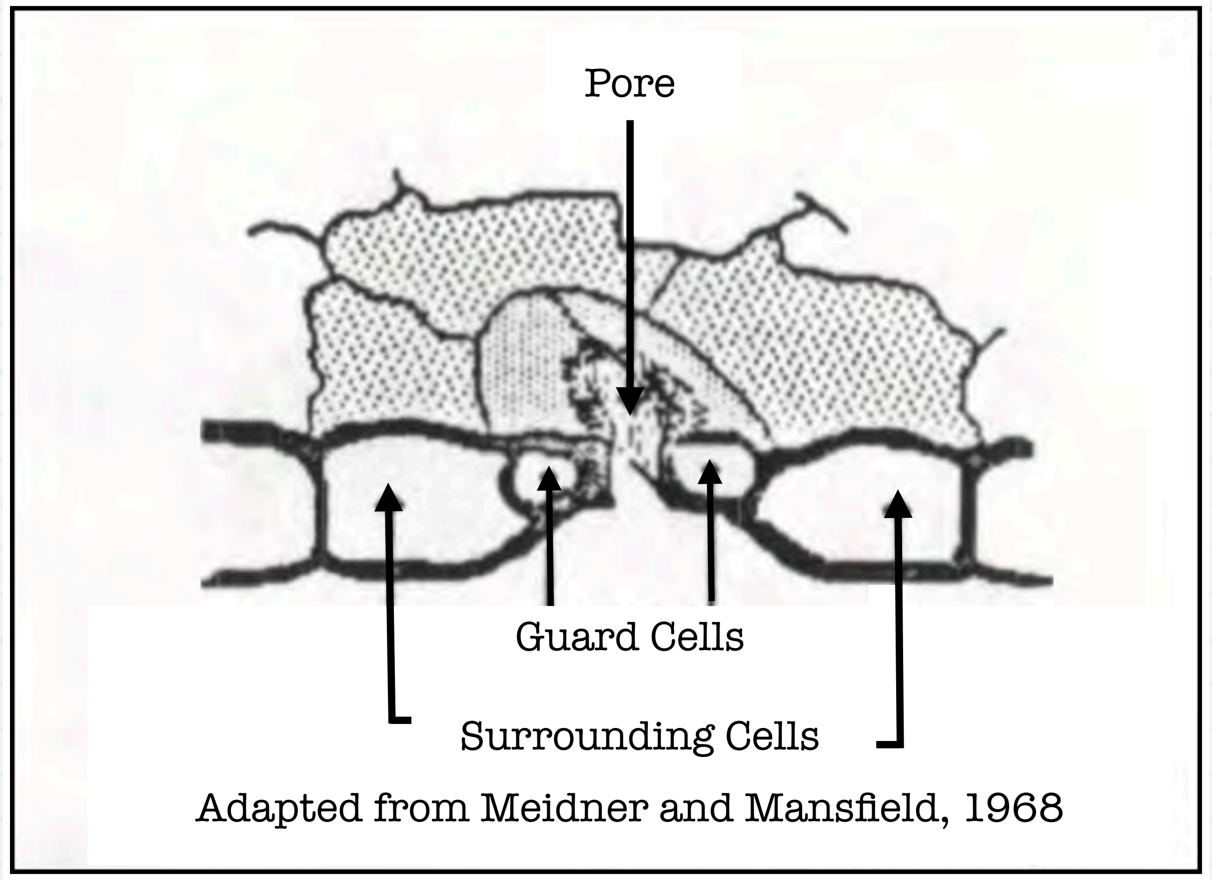




* Because the enclosed volume of the guard cell
* is much smaller than the enclosed volume of the surrounding cell,
* movement of a given amount of water between the two produces differing internal pressure changes, i.e., the surrounding cell pressure will change less than the guard cell pressure.

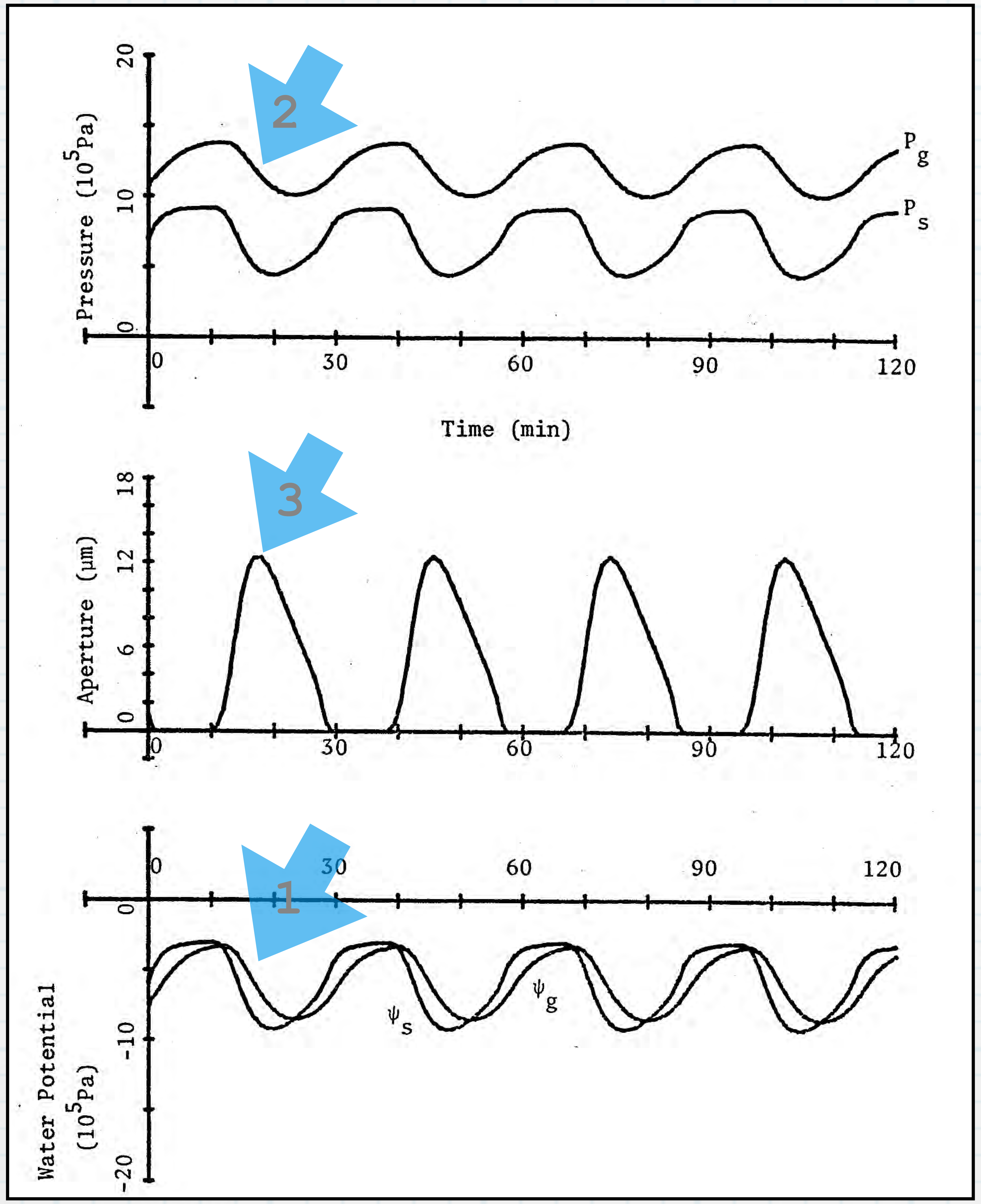
Importance of micelle for time-dependent conditions (2)





* Consequently, the stiffening provided by the micelle allows a smaller pressure increase in the surrounding cell to reverse the width adjustment of a larger pressure increase in the guard cell. [With micelle, a pore width increase due to a guard cell pressure increase might be counteracted by half that pressure increase in the surrounding cell.]
* A static, doubly-elliptical guard cell geometric structure can open the pore with or without radial stiffening by micelle. (But micelle do improve the static response.) HOWEVER, the micelle are vital for the stoma's dynamical response.

Periodic Response

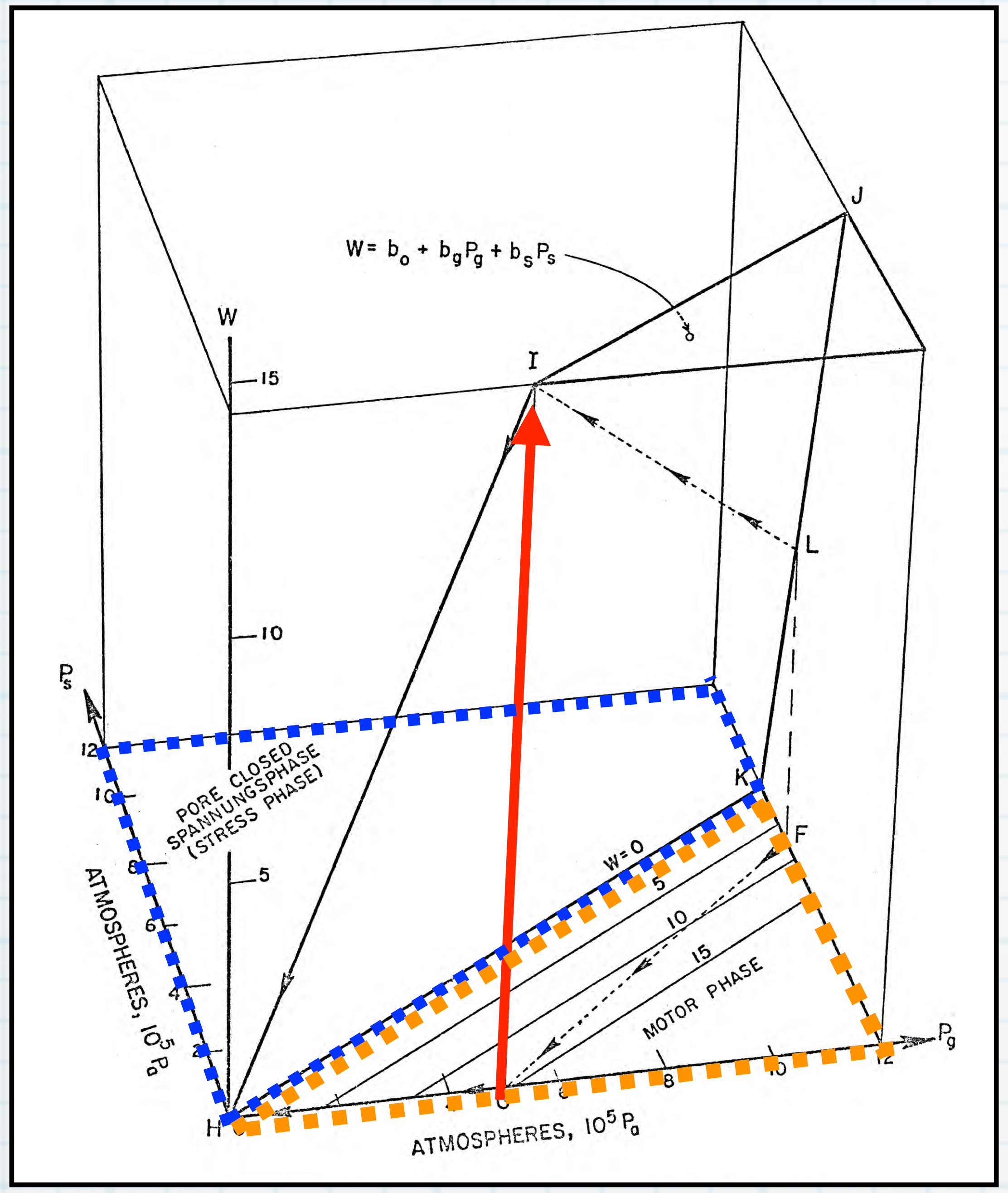


* 1. Under certain conditions, if the water potential in the guard and surrounding cells are out of phase in a particular manner,

* 2. the pressures in the guard and surrounding cells oscillate out of phase.

* 3. Then, a periodic opening and closing of the stoma can occur.

Periodic Response

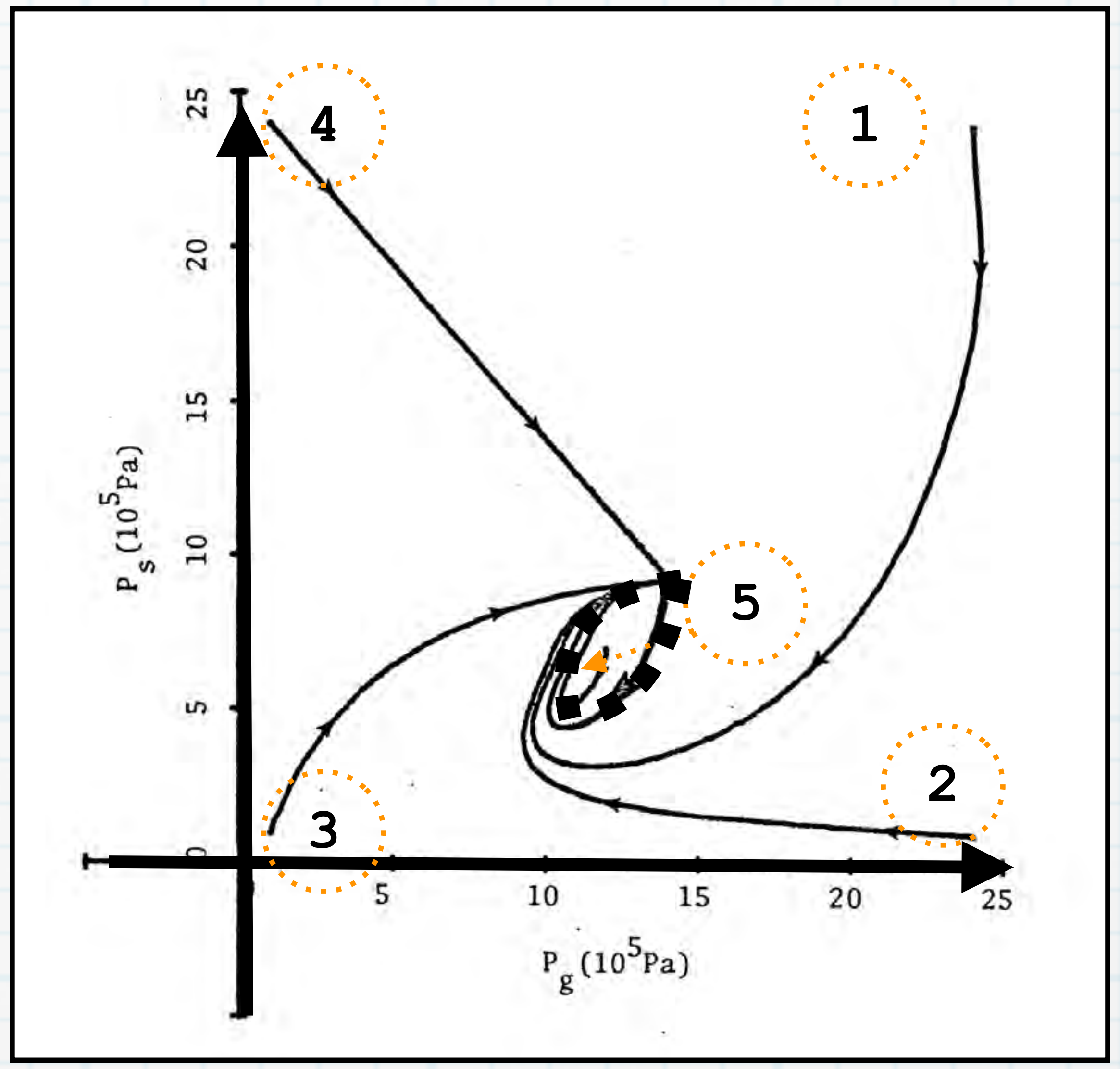


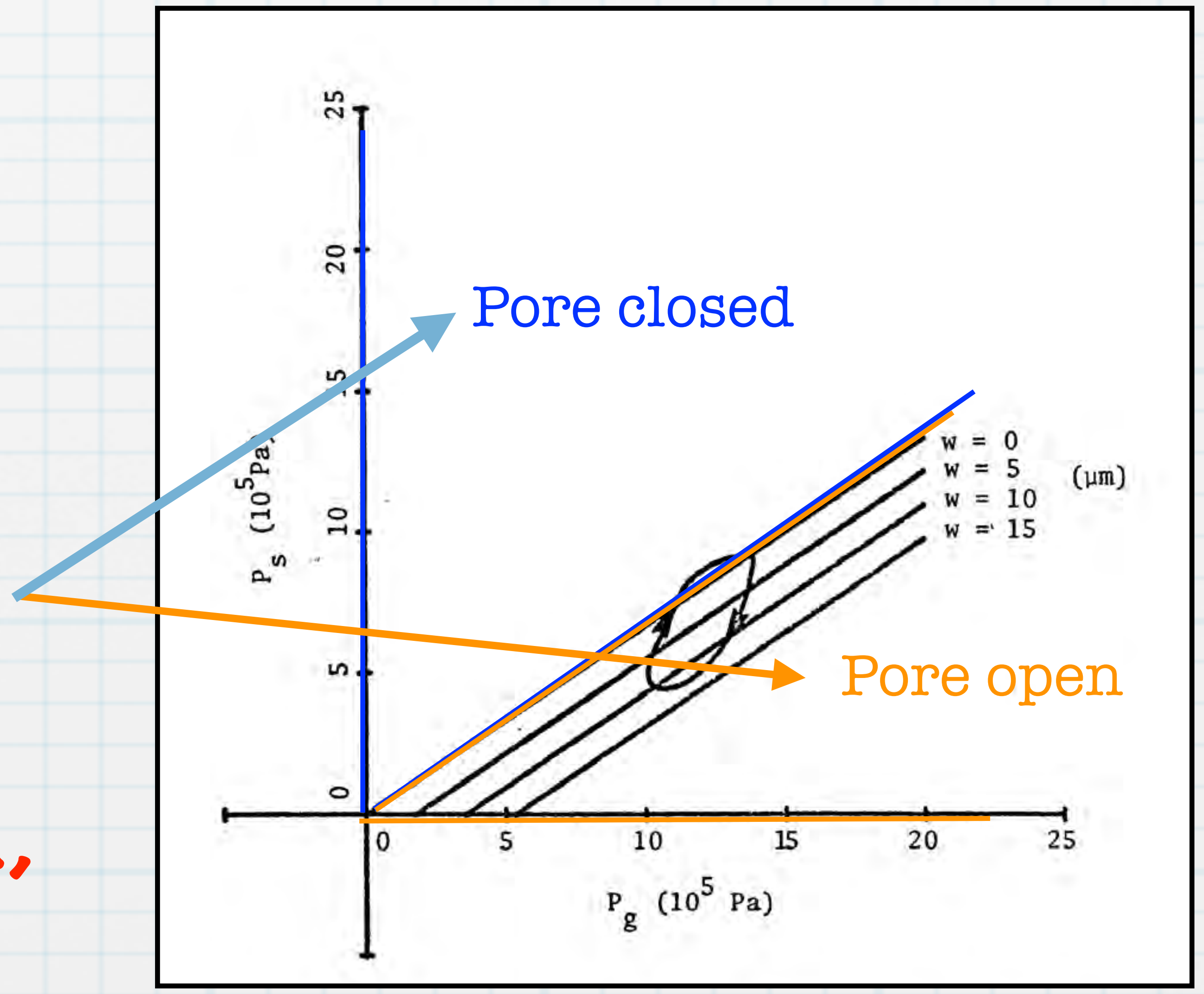
Graphs at right have the same axes as at left:

Pore is closed for these pressure combinations.

Pore is open for these pressure combinations.

Height above (Pg, Ps) plane is the pore width.



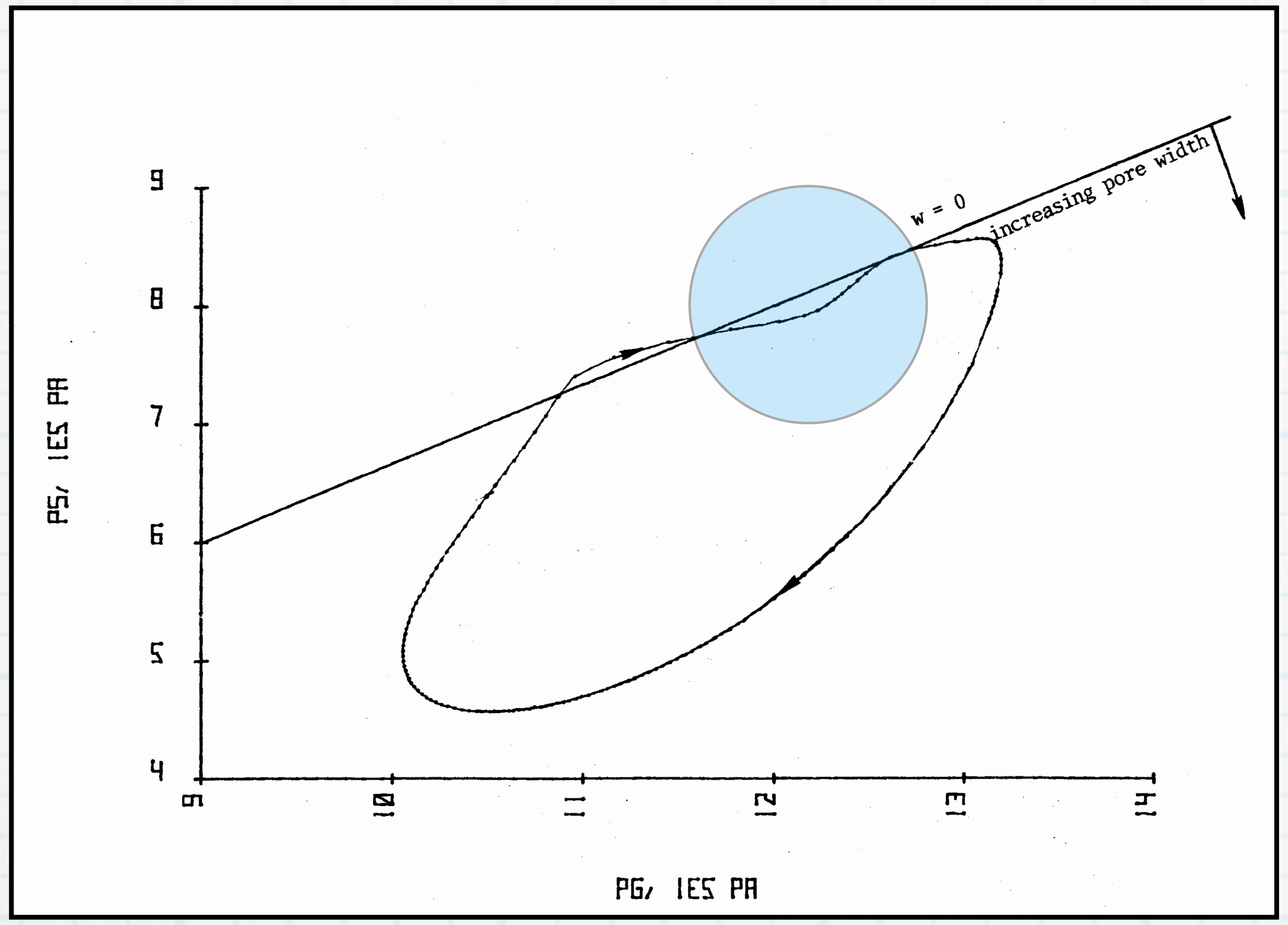


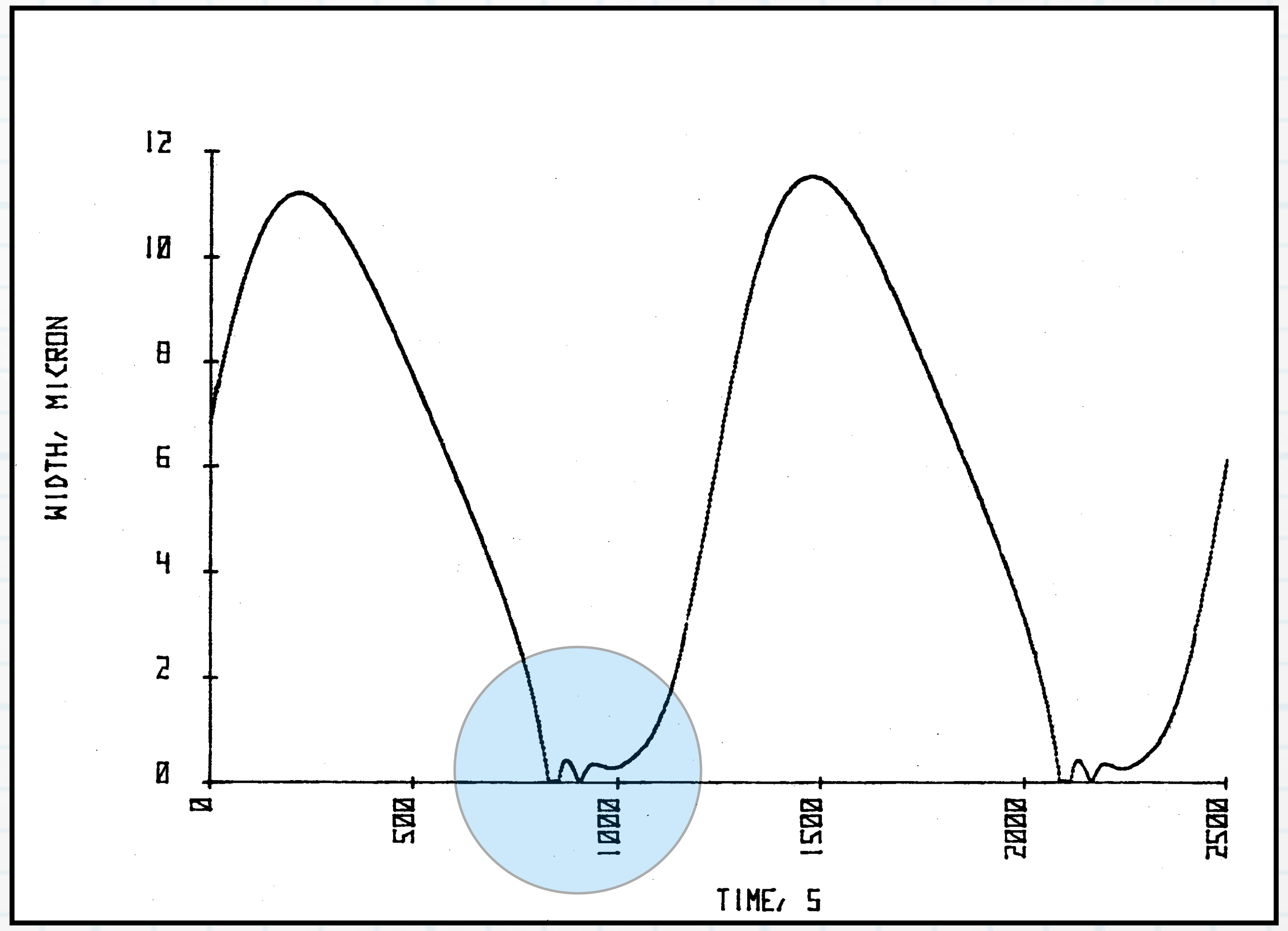
- For stable limit cycle conditions,
- any (Pg,Ps) starting point leads to the same repetitive cycle.
- Different equations apply to each of these regions. (This leads to an endogenous rhythm, i.e., a stable limit cycle.)

Model for Periodic Response

Periodic Opening, INCLUDING Carbon Dioxide

Upadhyaya, S.K., R.H. Rand, and J.R. Cooke. 1983. A mathematical model of the effects of carbon dioxide on stomatal dynamics. J. Theor. Biol. (1983) 101: 415-440.





- With an added carbon dioxide feedback loop, an additional pore width oscillation (shorter, say 2 min) occurs, but only when the pore is nearly closed.
- When CO_2 is depleted, the pore opens briefly (allowing it to be replenished).
- This behavior yields an improved water use efficiency!

Conclusions - 1

(system dynamics)

1. Stomatal opening proceeds in two distinct phases - a stress phase (width = 0) and a motor phase (width > 0). These two regions are explicitly identified for the Pg-Ps plane.

2. The micelle play a prominent role in the dynamical behavior by allowing smaller pressure changes in the surrounding cell to counteract the larger pressure changes in the guard cell.

3. When the pore opens, diffusion from the sub-stomatal cavity decreases the subsidiary cell pressure, causing the pore to "pop" open. [This rapid response occurs without changes in guard cell solute content, i.e., without invoking hydroactive conditions.]

Conclusions - 2

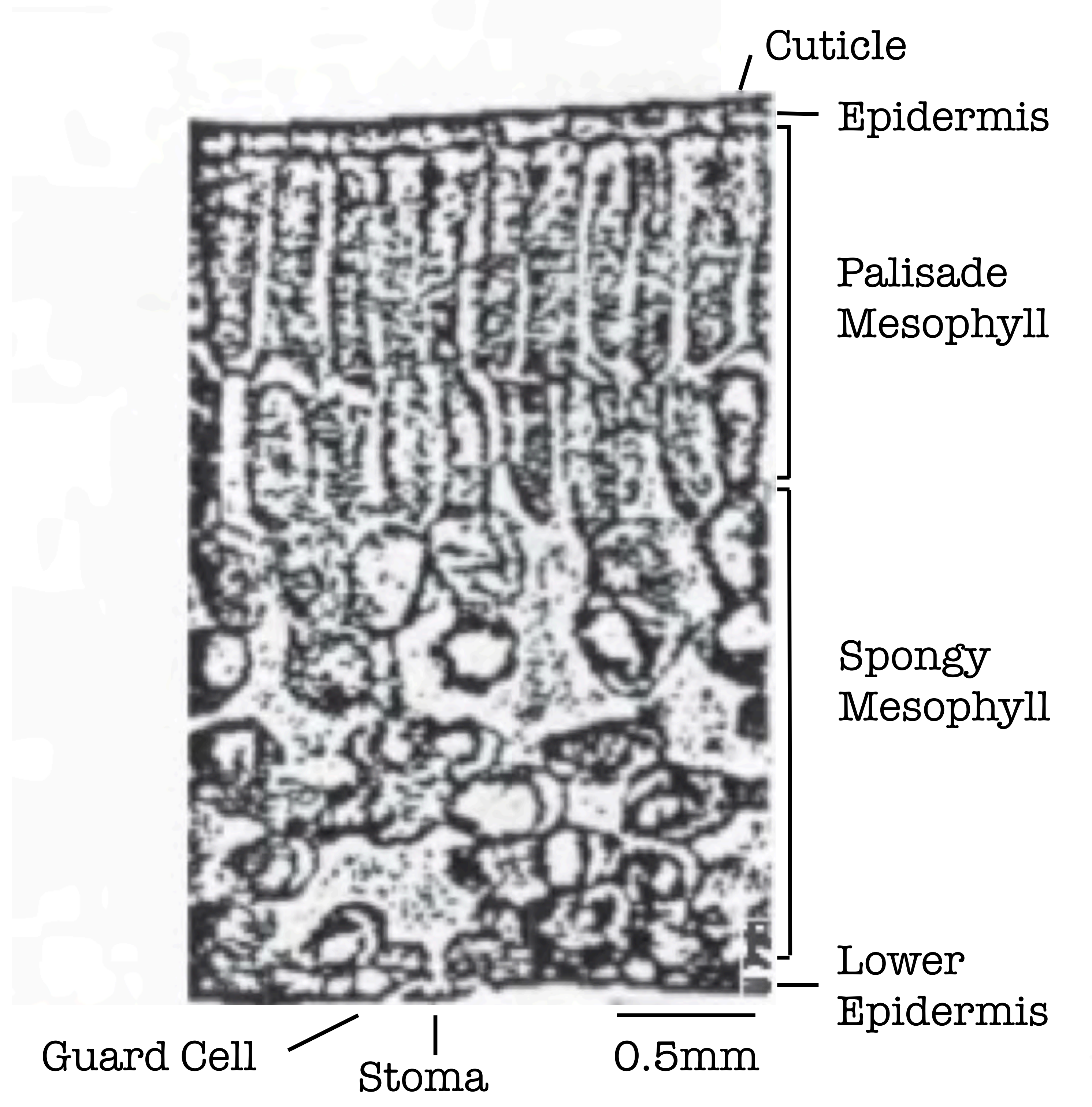
(system dynamics)

4. Stable, hydraulically based pore width oscillations can occur. Under stable limit cycle conditions, the oscillatory cycle is independent of initial conditions. [These oscillations constitute an endogenous rhythm.]

5. With a carbon dioxide loop added, an additional, shorter period oscillation can occur when the pore would otherwise be closed. This allows an additional uptake of CO_2, and enhances water use efficiency.

General Summary

* A leaf is an enclosed biological structure that provides a stable environment for photosynthesis.
* Higher plants could colonize the land only after a barrier to water loss (the cuticle) existed.
* Stomata provide a mechanism for the regulation of gaseous exchange through the cuticle.



Adapted from Keeton and Gould, 4th edition. p 274, 1986

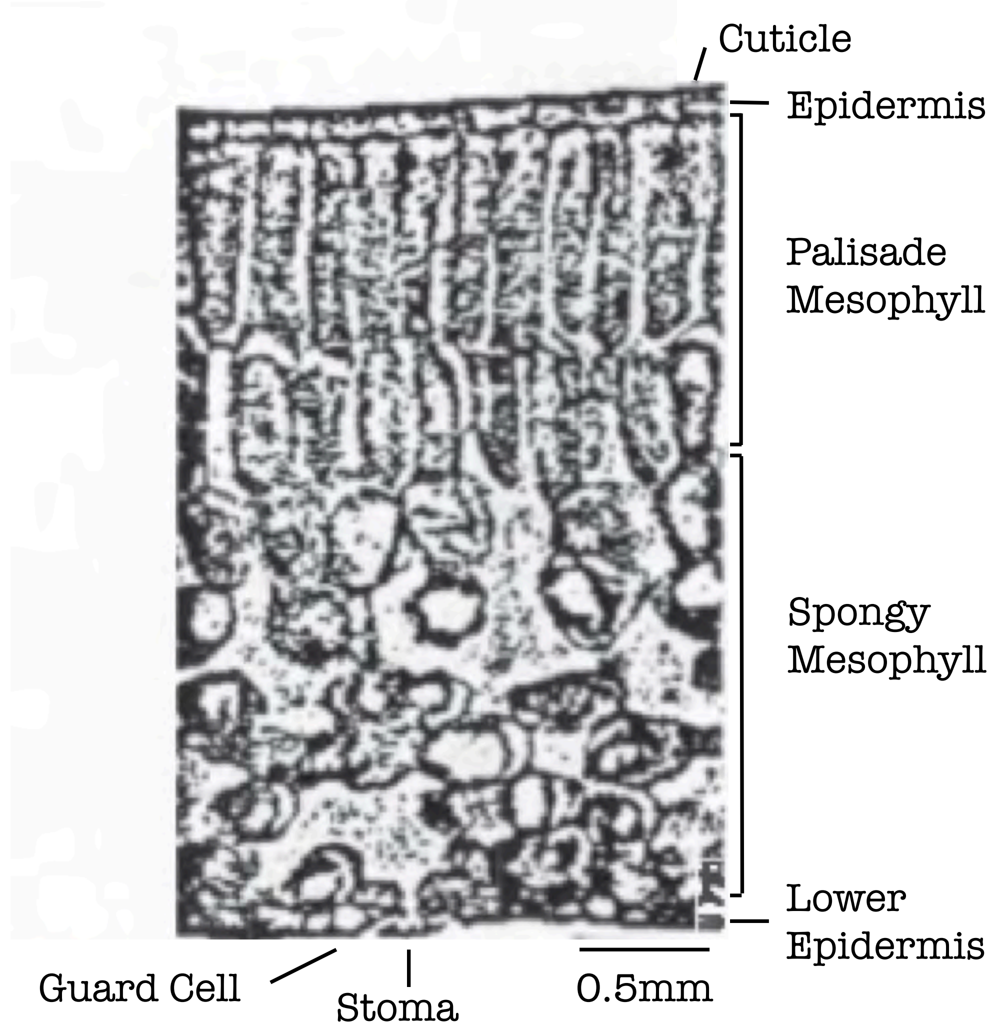
Conjectures

(NOT Conclusions)

1. Can crops be modified to function successfully despite climate change?

Some plants (C4) could benefit from higher levels of carbon dioxide. But stomata close under high CO_2 levels, limiting its uptake, e.g., with greenhouse-produced lettuce.

1. Having a more permeable cuticle or more closely spaced stomata might be advantageous for plants grown within high-humidity, controlled environments (that is, to enable an increased carbon dioxide uptake without incurring a water loss penalty).



Adapted from Keeton and Gould, 4th edition. p 274, 1986

2. Can crops be modified to function successfully despite climate change?

Some crops, such as cotton, are better adapted to drought stress than others. Cotton exhibits an oscillatory stomatal response when under drought stress (with a period of about 20-30 minutes).

Both photosynthate production and water loss would be decreased under these conditions, but the plant might survive without supplemental water. Water use efficiency might be improved too.

3. Can crops be modified to function successfully despite climate change?

Under severe climate-limiting conditions, rather than maximizing applied resources for highest crop yields, a strategy for functioning within available resources might become necessary.

Could this beneficial "limit cycle" behavior in cotton (when under stress) be exploited with other crops too?

4. Can crops be modified to function successfully despite climate change?

When hay is harvested, but before storage, a drying period is necessary to avoid spoilage. Could this weather-sensitive drying period be shortened if stomata of the detached leaves were caused to remain open after being cut?

Some geographical areas are limiting the watering of lawns. Could water be saved if shorter lawn grasses were used, e.g., sufficiently short to avoid the need for mowing, and thereby avoiding the water loss through the severed leaves that remain attached to the plant?

5. Can crops be modified to function successfully despite climate change?

(More on watering.)

If a plant's photosynthate production rate were intentionally slowed, e.g., a less permeable cuticle, a sparser stomatal density, or even using sunken stomata (found in some desert plants) to create a thicker boundary layer, could the need for irrigation water be reduced?

5. Resources

Additional (open access) background resources:
https://hdl.handle.net/1813/45423

See the following collections:
01_StomatalControl
02_PlantBiomechanics

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