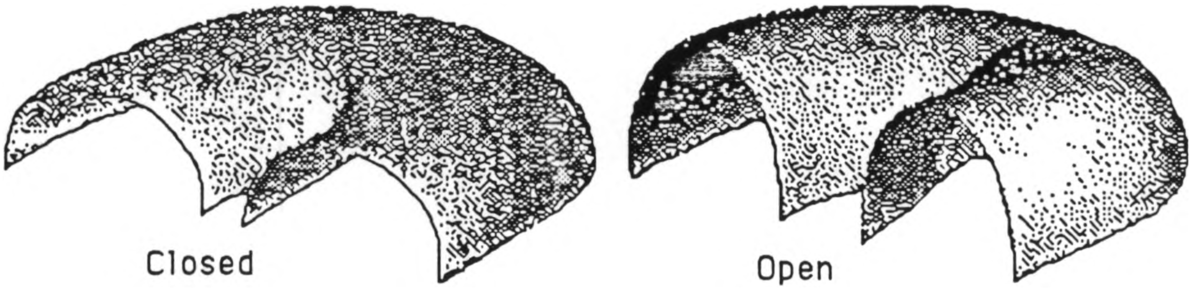
StomateTutor™

An Introduction to Stomatal Control of Gas Exchange in Plants

version 2.0



Content

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StomateTutor™ : An Introduction to Stomatal Control of Gas Exchange in Plants (Version 2.0)

This is a HyperCard implementation which includes Pascal programs. HyperCard, which requires at least 1 Megabyte of memory, must be supplied by the user. The system disk must include the Geneva 10 pt font. When using, open the HyperCard stack *StomateTutor* which coordinates the remaining files (StomateTutor1-3 and the two Pascal programs). When you run StomateTutor the first time with your file configuration, you must locate the Pore Width and Diffusion applications used in Modules 1 and 2, respectively.

Abstract:

Stomata are the microscopic pores created by a pair of guard cells on the plant surfaces, especially leaves, which open and close to regulate gas exchange in plants. This contemporary presentation of the century-old topic of stomatal control of gas exchange in plants uses HyperCard and integrated Pascal applications to present ideas visually. Hypertext allows this courseware to be user-adjusted for novice, intermediate, or advanced levels. The Pascal applications, which are launched from within HyperCard, allow the student to manipulate three-dimensional images to improve visualization and to perform computational experiments without explicitly dealing with the mathematics, which might otherwise be intimidating to undergraduate students. The student can simulate experiments which would be prohibitively expensive and time consuming to conduct in an undergraduate lab.

Research interest in stomata continues unabated after more than a century. Several thousand papers are published each year which explicitly deal with some aspect of stomatal action because this topic is critical to photosynthesis and crop production.

The field of biology does not yet utilize mathematics and computers as extensively as do the physical sciences. Consequently, mathematically based research may be neither understood nor appreciated in the plant sciences. This courseware grew out of a desire to communicate our own mathematical research in a manner which could be readily understood by a non-mathematically oriented audience.

The segment of a general biology course dedicated to gas exchange is often quite abbreviated. Therefore, this material must be presented in a compact, yet comprehensible form. The learning time has been compressed.

We present a contemporary view of the physical aspects of stomatal control of gas exchange in plants and identify departures from traditional explanations. We wish to stimulate interest in this topic and in the use of mathematics and computers—under-utilized resources in biology. We also wish to make this an enjoyable learning experience. This is a comprehensive and coherent treatment of a set of related research topics.

1. Our finite element stress analysis of guard cells demonstrates the inadequacies of the explanation found in all undergraduate textbooks. Guard cell geometry, not differential wall thickness, is the central structural feature. Pore opening and closing are shown to involve a three-dimensional deformation which results from the opposing guard cell and surrounding cell pressures. The radial stiffness of the guard cells improves the effectiveness of these pressure interactions, although the pore would still open without this structural component.

2. We show that the average stomatal pore spacing common to most species permits the highest possible rate of gas exchange attainable *without* subjecting the plant's internal gaseous environment to unacceptable fluctuations due to ordinary wind speed changes. In other words, closer stomatal spacing would allow a higher rate of gas exchange, but the plant's stomatal control system could not respond rapidly enough to maintain a constant internal environment for photosynthesis. Wider spacing would lead to a more stable internal environment, but at the expense of a lower rate of photosynthesis. This has implications for the genetic adaptation of stomatal spacing to match environmental conditions.

3. We identify the mechanism which permits rapid pore opening when environmental changes occur. When guard cell pressure increases enough to initiate pore opening, evaporative water loss from the stomatal cavity wall reduces surrounding cell pressure, which produces pore opening. This reduction in surrounding cell pressure, rather than the further increase in guard cell pressure, is responsible for the rapid opening. Unfortunately, biochemical studies of stomatal action have concentrated almost exclusively upon the membrane between the guard

and surrounding cells, rather than upon the properties of the control system.

4. Finally, we present possibly the first definitive explanation of an endogenous rhythm in plant biology—a periodic opening and closing of stomata under constant environmental conditions. [Superficially an endogenous rhythm could be regarded as a response without a stimulus.] Not only does this module identify the mechanism, but we also conjecture that a potentially practical use of this phenomenon is the reduction in irrigation costs. Our studies suggest that water use efficiency is increased during these periodic oscillations. In other words, the ratio of carbon dioxide intake to water vapor loss is improved, although the rate of photosynthate production is lowered. These oscillations are known to occur naturally during stress conditions. Perhaps we can find ways to deliberately induce these oscillations in order to improve water utilization.

Pedagogical Considerations

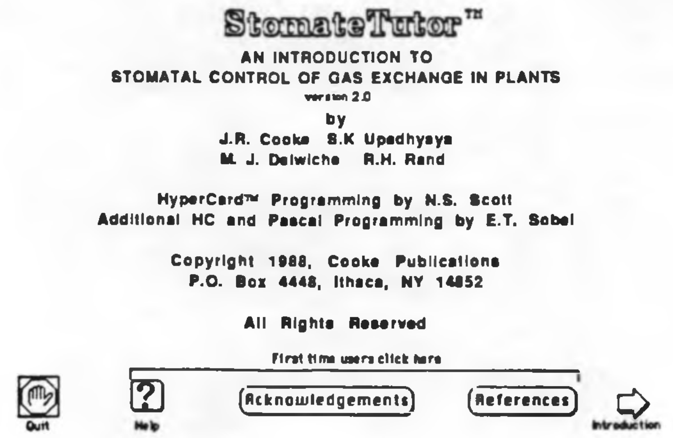
Undergraduates in introductory biology and advanced undergraduates in plant physiology courses are the intended audience. We assume that these students have had very limited mathematical and computer experience. The mathematical content is also appropriate for applied mathematics students.

HyperCard allows the student to adjust the level of detail presented. Annotations (Elementary, Intermediate, and Advanced) indicate the recommended paths to follow according to your biological preparation. By launching Pascal programs from within HyperCard, we greatly extended the flexibility of HyperCard. This allows the courseware to be even more responsive to the student. The performance of calculations and the generation of user-defined graphics without the explicit consideration of the mathematical equations significantly extends the range of uses and users. Hypotheses not presented by the authors can be invented and tested by the student without facing the chore of writing a program in a high level programming language.

HyperCard is a powerful tool so we needed only one unique extension. We created a bookmark. When the student terminates a session, an opportunity is presented for a marker to be created. A bookmark icon appears on the title screen when the session is resumed and allows an immediate return to the point of previous study.

Much of this material could be presented effectively in the print format; see the enclosed reprint. However, traditional print media allows, but does not necessarily encourage extensive usage of graphics to support the text. Incontrast, this Macintosh environment encourages the use of graphics. Compare the ratio of text to graphics in the two presentations. Such extensive reliance upon graphics in a traditional presentation would be abnormal.

Snapshots of the HyperCard stacks and the Pascal applications follow.



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AN INTRODUCTION TO STOMATAL CONTROL OF GAS EXCHANGE IN PLANTS

version 2.0

by

J.R. Cooke S.K Upadhyaya
M. J. Delwiche R.H. Rand

HyperCard™ Programming by N.S. Scott
Additional HC and Pascal Programming by E.T. Sobel

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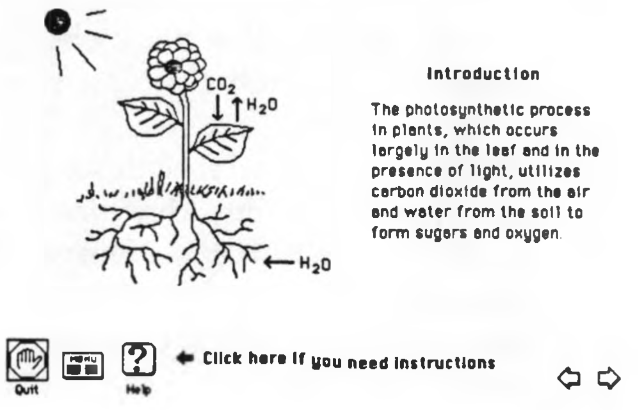
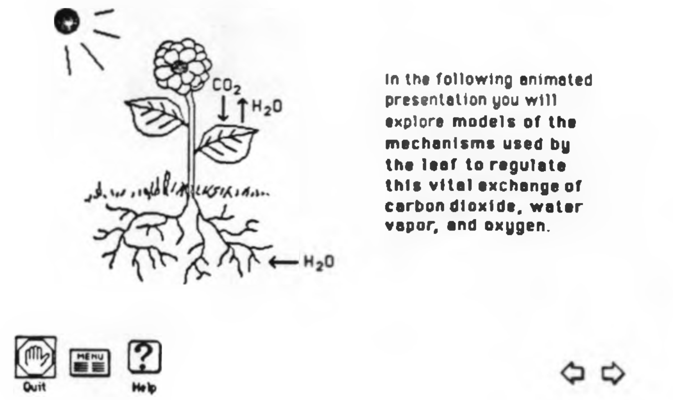
First time users click here



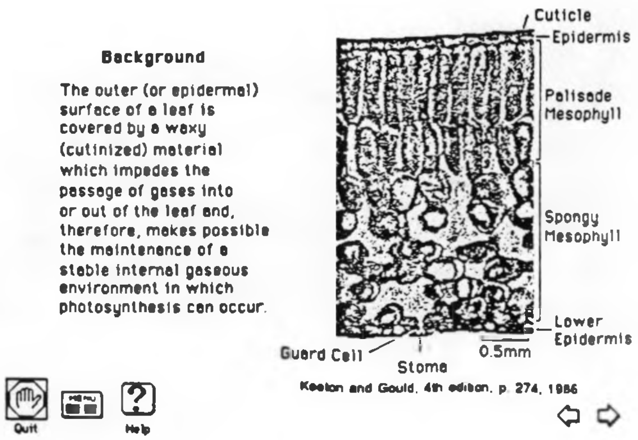
Introduction

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

Click here if you need instructions



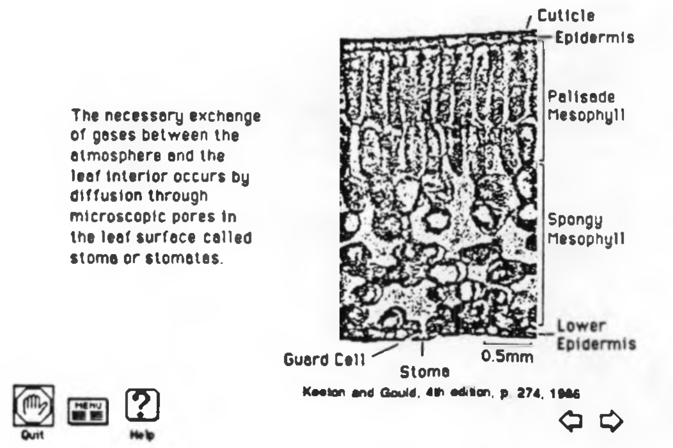
In the following animated presentation you will explore models of the mechanisms used by the leaf to regulate this vital exchange of carbon dioxide, water vapor, and oxygen.



Background

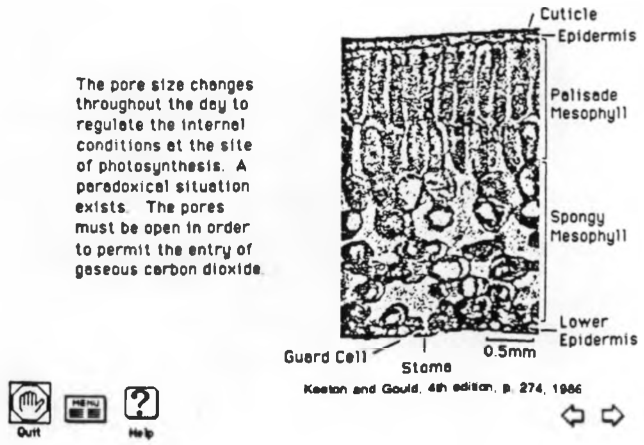
The outer (or epidermal) surface of a leaf is covered by a waxy (cutinized) material which impedes the passage of gases into or out of the leaf and, therefore, makes possible the maintenance of a stable internal gaseous environment in which photosynthesis can occur.

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



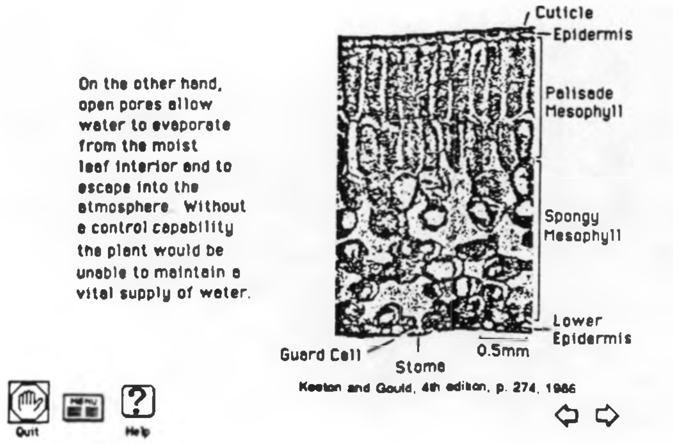
The necessary exchange of gases between the atmosphere and the leaf interior occurs by diffusion through microscopic pores in the leaf surface called stoma or stomates.

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



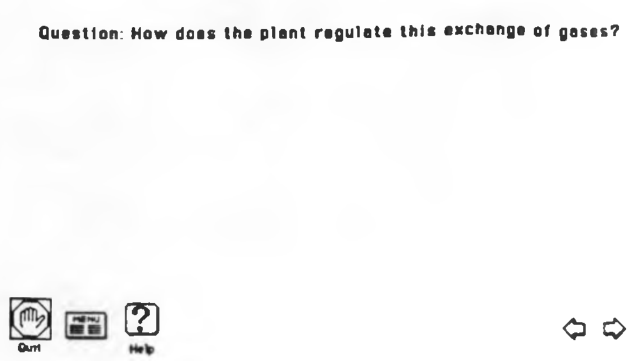
The pore size changes throughout the day to regulate the internal conditions at the site of photosynthesis. A paradoxical situation exists. The pores must be open in order to permit the entry of gaseous carbon dioxide.

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

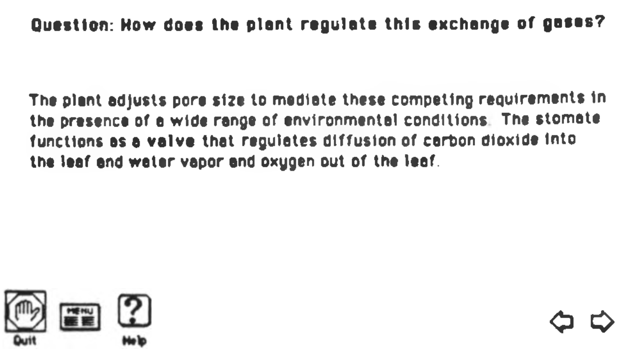


On the other hand, open pores allow water to evaporate from the moist leaf interior and to escape into the atmosphere. Without a control capability the plant would be unable to maintain a vital supply of water.

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

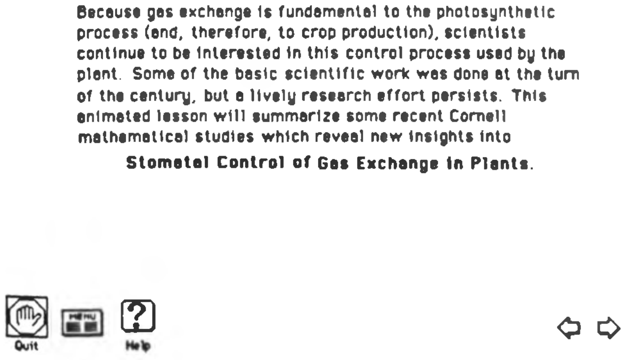


Question: How does the plant regulate this exchange of gases?



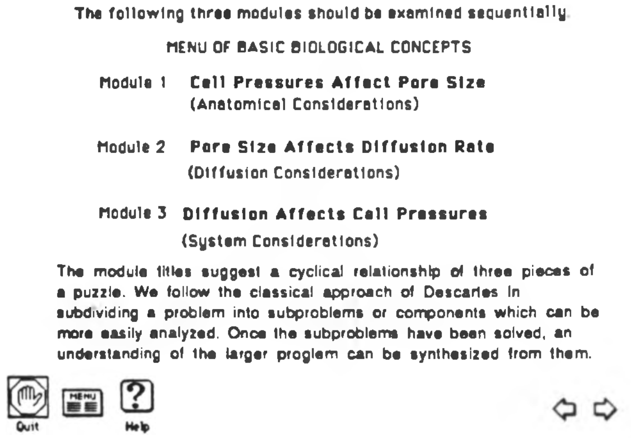
Question: How does the plant regulate this exchange of gases?

The plant adjusts pore size to mediate these competing requirements in the presence of a wide range of environmental conditions. The stomate functions as a valve that regulates diffusion of carbon dioxide into the leaf and water vapor and oxygen out of the leaf.



Because gas exchange is fundamental to the photosynthetic process (and, therefore, to crop production), scientists continue to be interested in this control process used by the plant. Some of the basic scientific work was done at the turn of the century, but a lively research effort persists. This animated lesson will summarize some recent Cornell mathematical studies which reveal new insights into

Stomatal Control of Gas Exchange in Plants.



The following three modules should be examined sequentially.

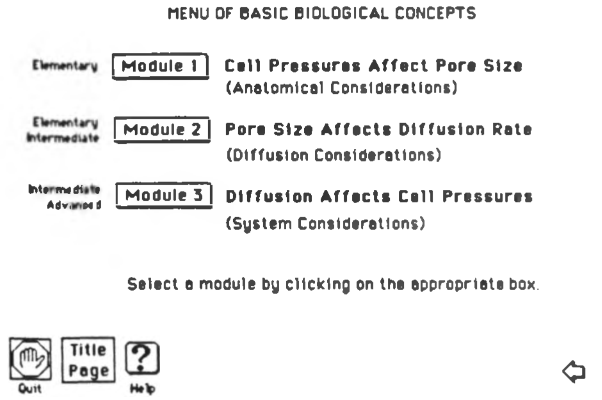
MENU OF BASIC BIOLOGICAL CONCEPTS

Module 1 **Cell Pressures Affect Pore Size**
(Anatomical Considerations)

Module 2 **Pore Size Affects Diffusion Rate**
(Diffusion Considerations)

Module 3 **Diffusion Affects Cell Pressures**
(System Considerations)

The module titles suggest a cyclical relationship of three pieces of a puzzle. We follow the classical approach of Descartes in subdividing a problem into subproblems or components which can be more easily analyzed. Once the subproblems have been solved, an understanding of the larger proglem can be synthesized from them.



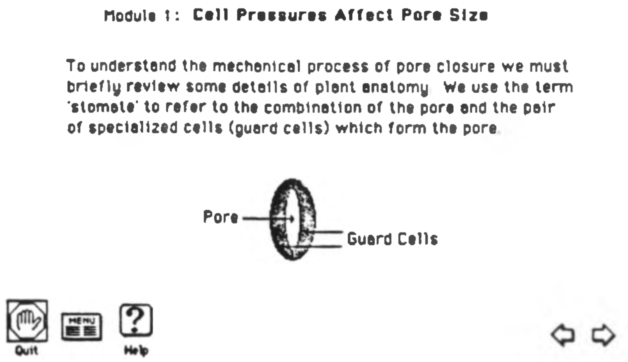
MENU OF BASIC BIOLOGICAL CONCEPTS

Elementary Module 1 **Cell Pressures Affect Pore Size**
(Anatomical Considerations)

Elementary Intermediate Module 2 **Pore Size Affects Diffusion Rate**
(Diffusion Considerations)

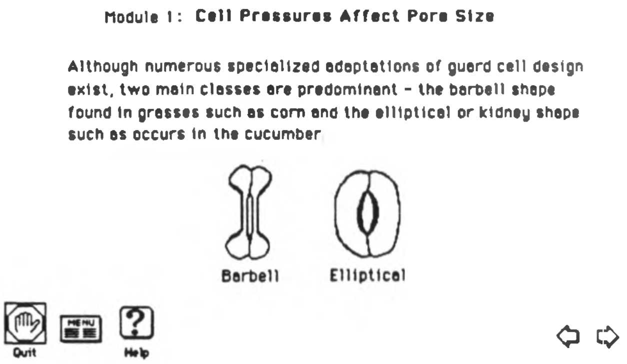
Intermediate Advanced Module 3 **Diffusion Affects Cell Pressures**
(System Considerations)

Select a module by clicking on the appropriate box.



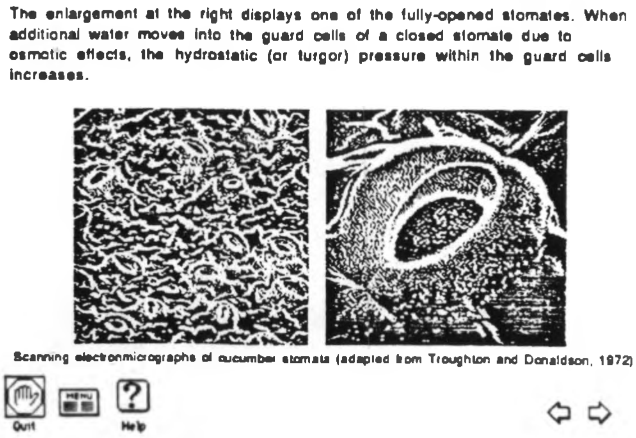
Module 1: **Cell Pressures Affect Pore Size**

To understand the mechanical process of pore closure we must briefly review some details of plant anatomy. We use the term 'stomate' to refer to the combination of the pore and the pair of specialized cells (guard cells) which form the pore.



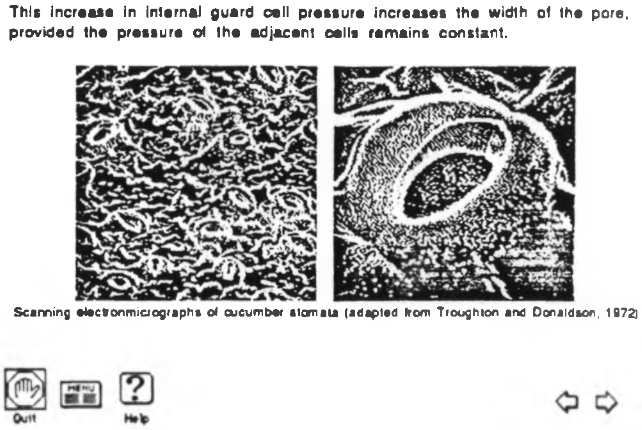
Module 1: **Cell Pressures Affect Pore Size**

Although numerous specialized adaptations of guard cell design exist, two main classes are predominant - the barbell shape found in grasses such as corn and the elliptical or kidney shape such as occurs in the cucumber.



The enlargement at the right displays one of the fully-opened stomates. When additional water moves into the guard cells of a closed stomate due to osmotic effects, the hydrostatic (or turgor) pressure within the guard cells increases.

Scanning electronmicrographs of cucumber stomata (adapted from Troughton and Donaldson, 1972)



This increase in internal guard cell pressure increases the width of the pore, provided the pressure of the adjacent cells remains constant.

Scanning electronmicrographs of cucumber stomata (adapted from Troughton and Donaldson, 1972)

Question: How does an increase in internal guard cell pressure increase the pore size?

Quit MENU ? Help ⇦ ⇨

Question: How does an increase in internal guard cell pressure increase the pore size?

Recent mathematical and computer studies in Biological Engineering provide fresh insight into this process. The traditional model of stomatal response attributes the opening of the pore to the expansion of guard cells away from each other because of an unequal thickness in their cell walls (Keeton and Gould. 1986. Biological Science, 4th ed, 276). After reviewing the traditional model, we present an alternative view.

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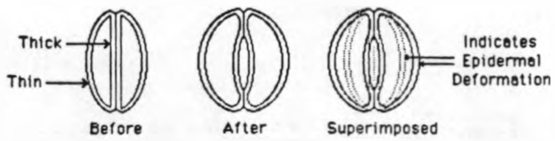
The Traditional Model



The wall of the guard cell forming the pore is thicker than the opposite wall where the guard cell joins the adjacent epidermal cells and formerly was believed to cause the guard cell to bulge into the surrounding cells.

This model implicitly assumes that a significant and unlikely stretching and shrinking of the epidermis occurs when pores open and close.

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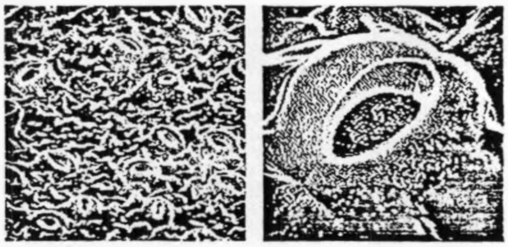
In the scanning electron micrographs of open cucumber stomata, the guard cell appears to be bulging out of the plane of the leaf. Of course, this could be an artifact of the gold plating process used to obtain the picture, but the results of the following mathematical analysis are consistent with these micrographs.



Scanning electronmicrographs of cucumber stomata (adapted from Troughton and Donaldson, 1972)

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Our mathematical studies indicate that guard cell deformation (and, hence, pore opening) results largely from the elliptical shape of the guard cells, not from differences in guard cell wall thickness.

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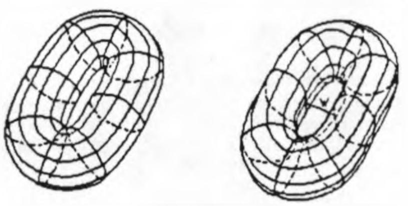
Let's review the results of the mathematical analysis



Consider a doubly elliptical torus of uniform wall thickness. When inflated, the pore increases in width as a result of a change in shape of the cell wall cross section.

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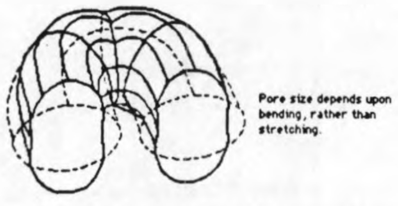
The perimeter of the transverse section of each guard cell remains essentially constant during the change in turgor pressure.



Elliptical torus (Cooke, et al., 1976)

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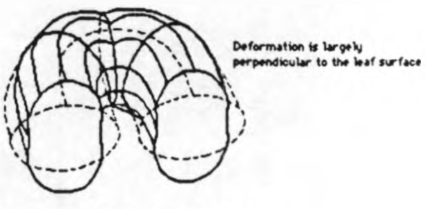
The dashed lines show the guard cell with low turgor pressure. In this condition the long axis of a guard cell's elliptical transverse section is parallel to the leaf surface.



Elliptical torus (Cooke, et al., 1976)

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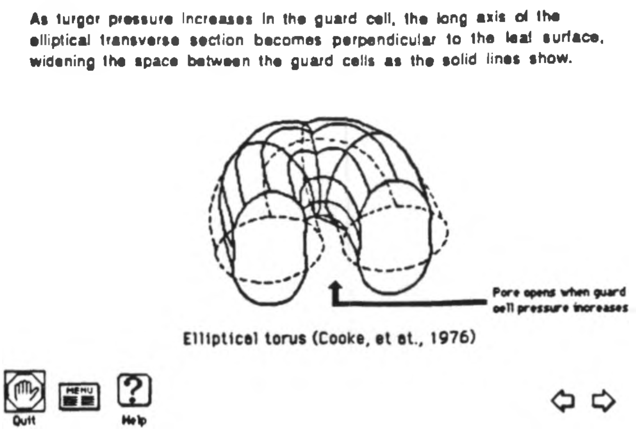
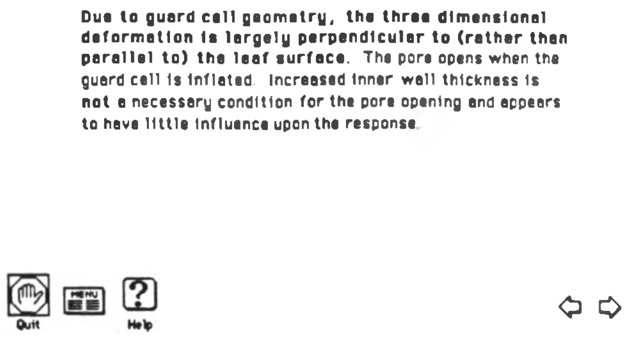
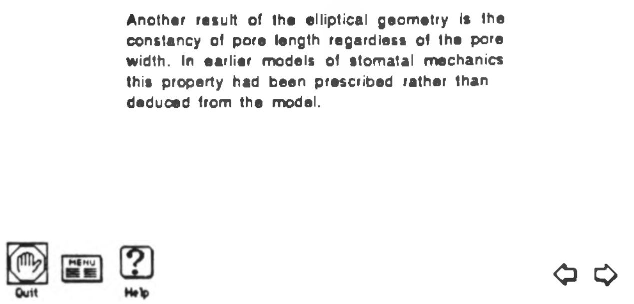
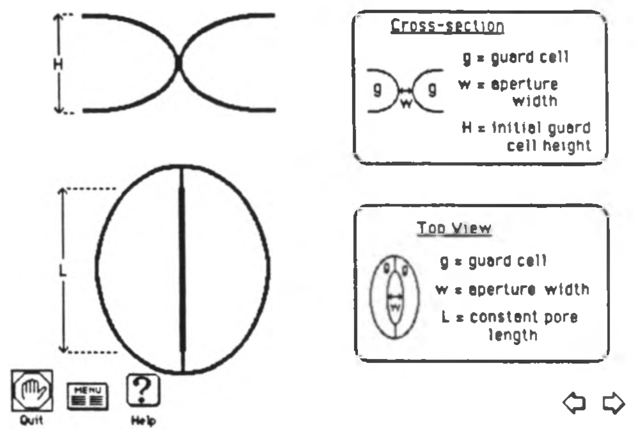

As turgor pressure increases in the guard cell, the long axis of the elliptical transverse section becomes perpendicular to the leaf surface, widening the space between the guard cells as the solid lines show.

Elliptical torus (Cooke, et al., 1976)


Due to guard cell geometry, the three dimensional deformation is largely perpendicular to (rather than parallel to) the leaf surface. The pore opens when the guard cell is inflated. Increased inner wall thickness is not a necessary condition for the pore opening and appears to have little influence upon the response.


Another result of the elliptical geometry is the constancy of pore length regardless of the pore width. In earlier models of stomatal mechanics this property had been prescribed rather than deduced from the model.

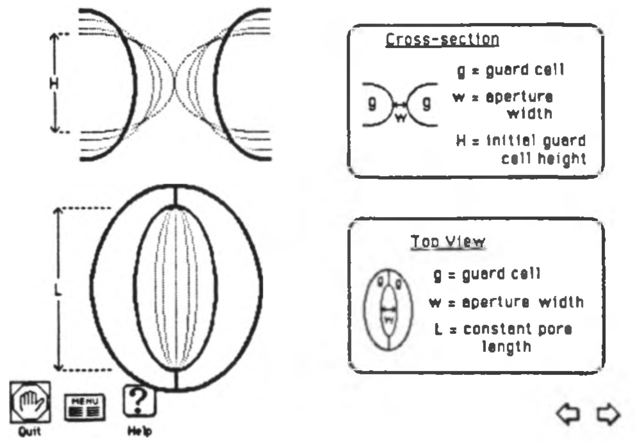


Cross-section

g = guard cell
w = aperture width
H = initial guard cell height

Top View

g = guard cell
w = aperture width
L = constant pore length



Cross-section

g = guard cell
w = aperture width
H = initial guard cell height

Top View

g = guard cell
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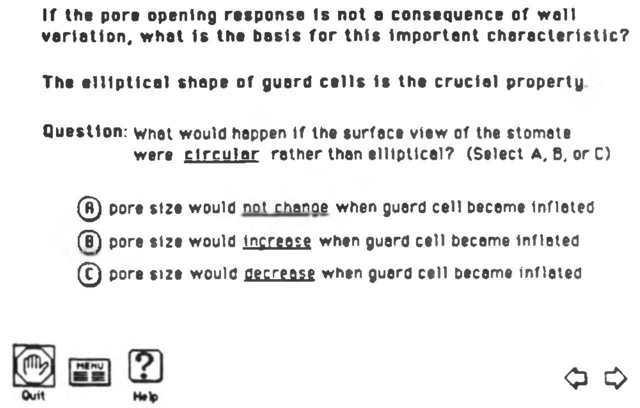
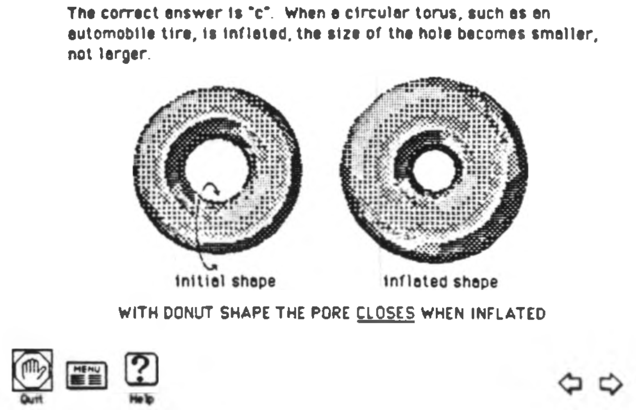
L = constant pore length


If the pore opening response is not a consequence of wall variation, what is the basis for this important characteristic?

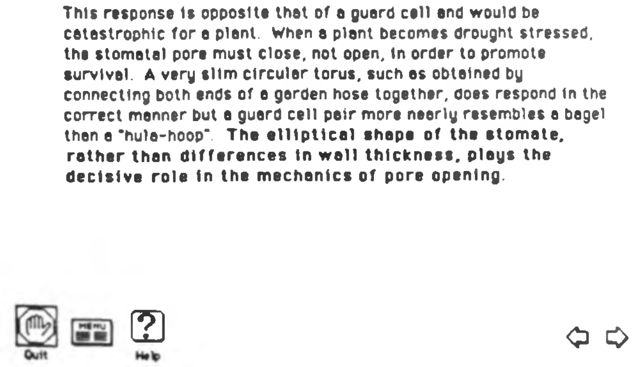
The elliptical shape of guard cells is the crucial property.

Question: What would happen if the surface view of the stomate were circular rather than elliptical? (Select A, B, or C)

Ⓐ pore size would not change when guard cell became inflated
Ⓑ pore size would increase when guard cell became inflated
Ⓒ pore size would decrease when guard cell became inflated


The correct answer is "c". When a circular torus, such as an automobile tire, is inflated, the size of the hole becomes smaller, not larger.

WITH DONUT SHAPE THE PORE CLOSES WHEN INFLATED


This response is opposite that of a guard cell and would be catastrophic for a plant. When a plant becomes drought stressed, the stomatal pore must close, not open, in order to promote survival. A very slim circular torus, such as obtained by connecting both ends of a garden hose together, does respond in the correct manner but a guard cell pair more nearly resembles a bagel than a "hula-hoop". **The elliptical shape of the stomate, rather than differences in wall thickness, plays the decisive role in the mechanics of pore opening.**

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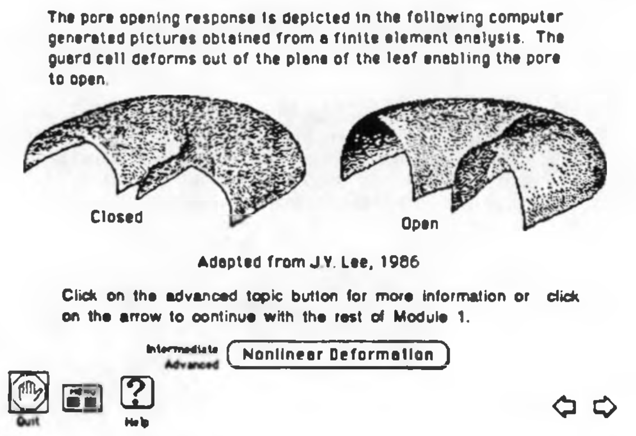


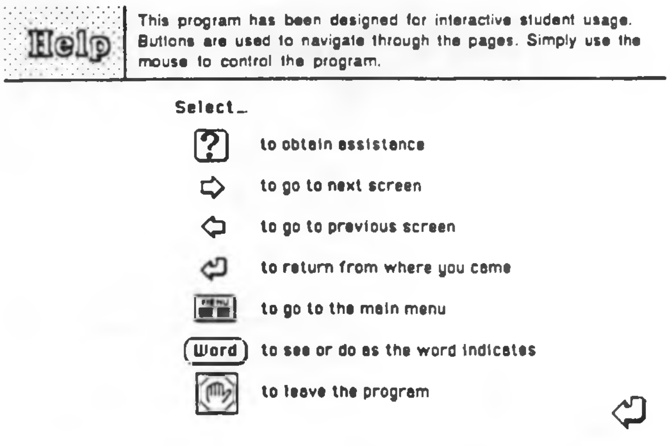
The pore opening response is depicted in the following computer generated pictures obtained from a finite element analysis. The guard cell deforms out of the plane of the leaf enabling the pore to open.

Closed

Open

Adapted from J.Y. Lee, 1986

Click on the advanced topic button for more information or click on the arrow to continue with the rest of Module 1.

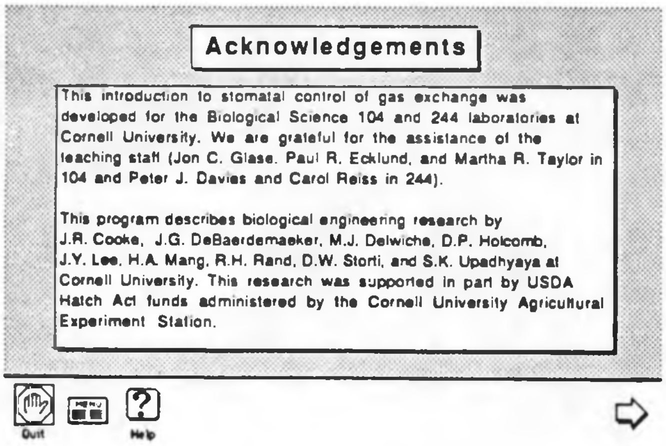


Help

This program has been designed for interactive student usage. Buttons are used to navigate through the pages. Simply use the mouse to control the program.

Select_

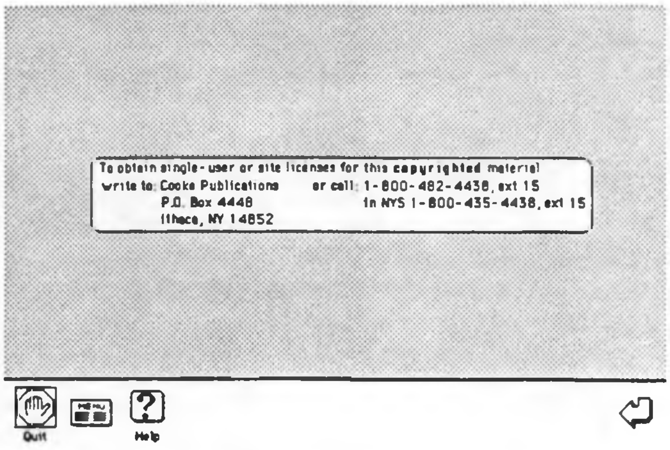
?	to obtain assistance
⇨	to go to next screen
⇦	to go to previous screen
⏎	to return from where you came
▦	to go to the main menu
Word	to see or do as the word indicates
✋	to leave the program



Acknowledgements

This introduction to stomatal control of gas exchange was developed for the Biological Science 104 and 244 laboratories at Cornell University. We are grateful for the assistance of the teaching staff (Jon C. Glase. Paul R. Ecklund, and Martha R. Taylor in 104 and Peter J. Davies and Carol Reiss in 244).

This program describes biological engineering research by J.R. Cooke, J.G. DeBaerdemaeker, M.J. Delwiche, D.P. Holcomb, J.Y. Lee, H.A. Mang, R.H. Rand, D.W. Storti, and S.K. Upadhyaya at Cornell University. This research was supported in part by USDA Hatch Act funds administered by the Cornell University Agricultural Experiment Station.



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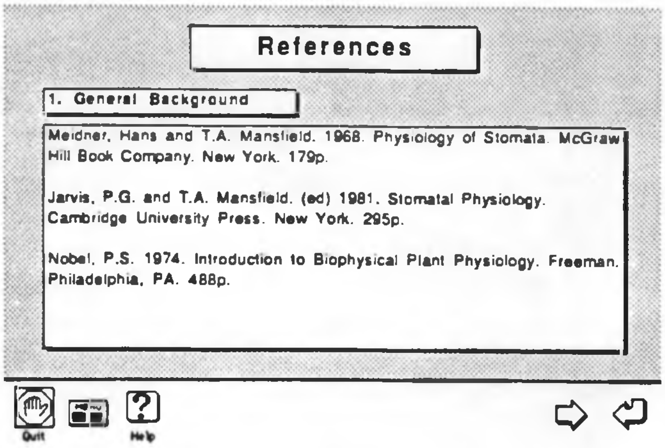

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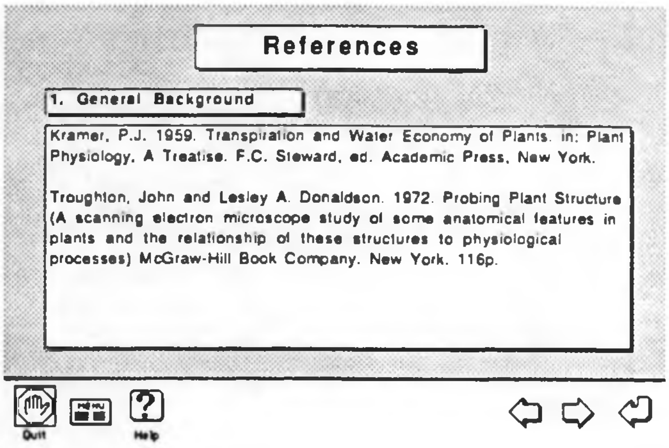

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1. General Background

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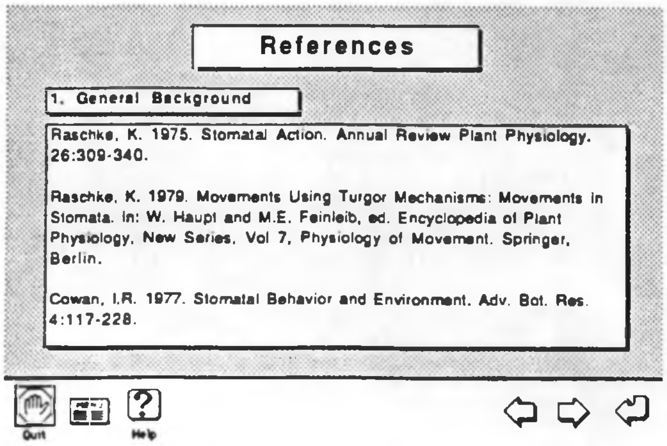

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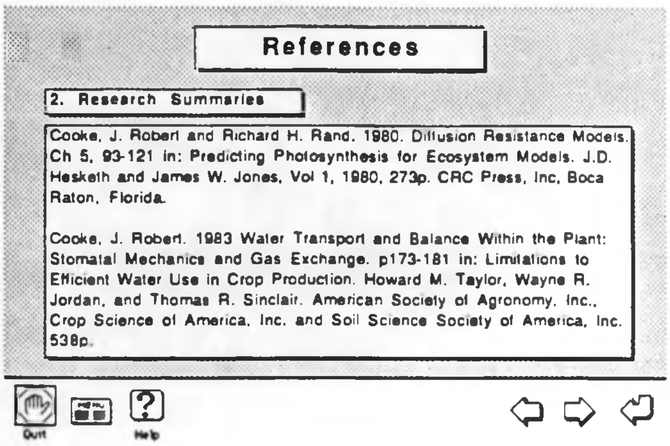

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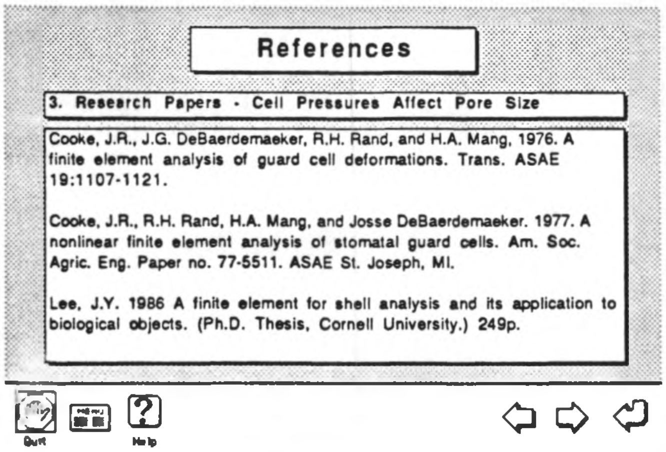

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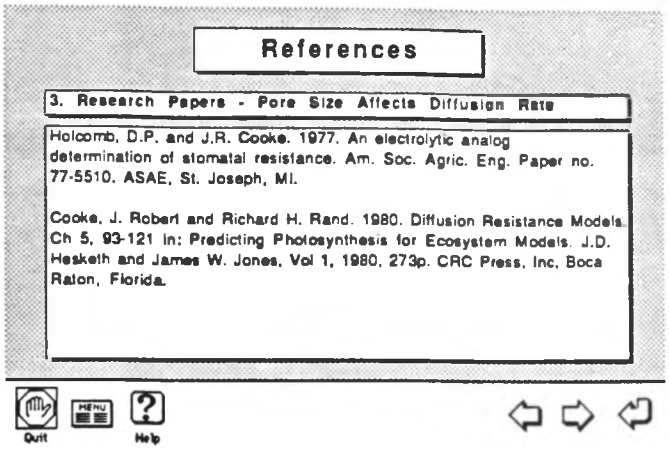

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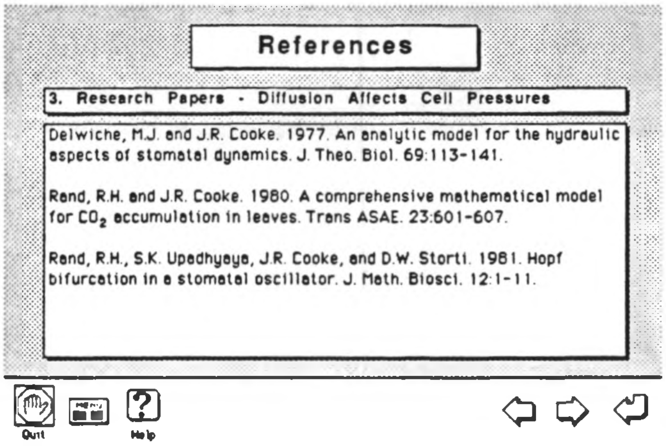

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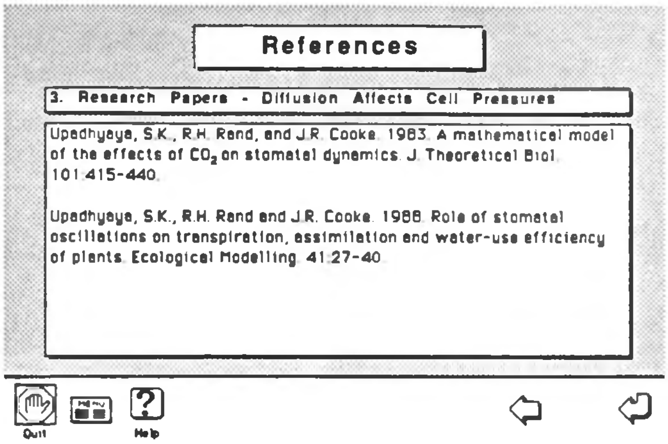

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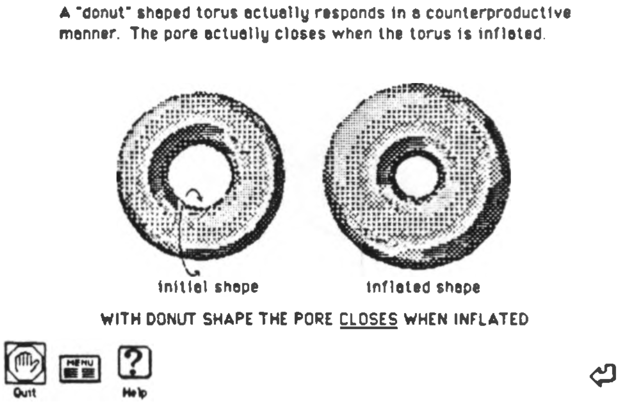
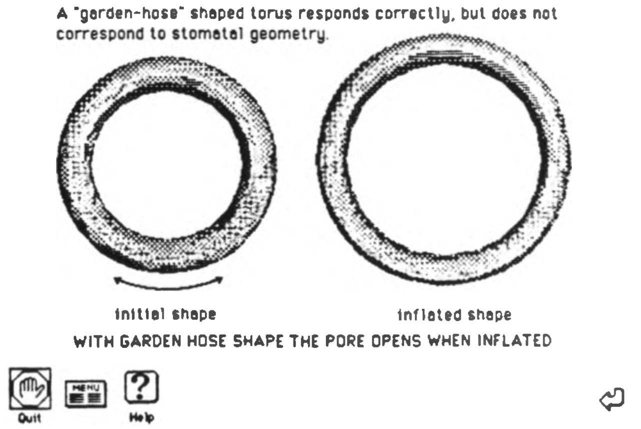


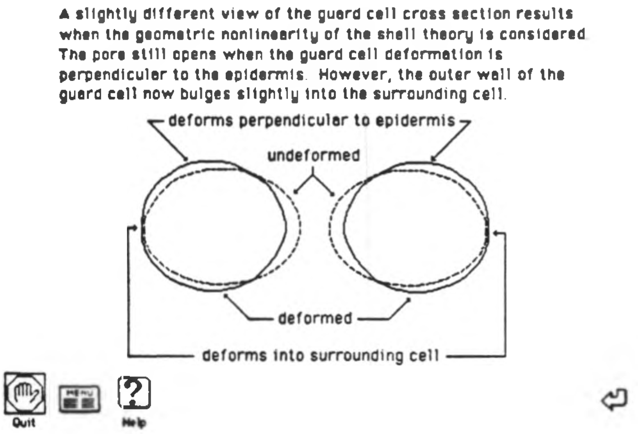
A "donut" shaped torus actually responds in a counterproductive manner. The pore actually closes when the torus is inflated.

WITH DONUT SHAPE THE PORE CLOSES WHEN INFLATED

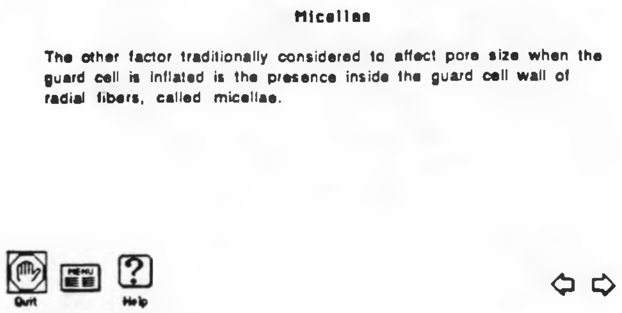


A "garden-hose" shaped torus responds correctly, but does not correspond to stomatal geometry.

WITH GARDEN HOSE SHAPE THE PORE OPENS WHEN INFLATED

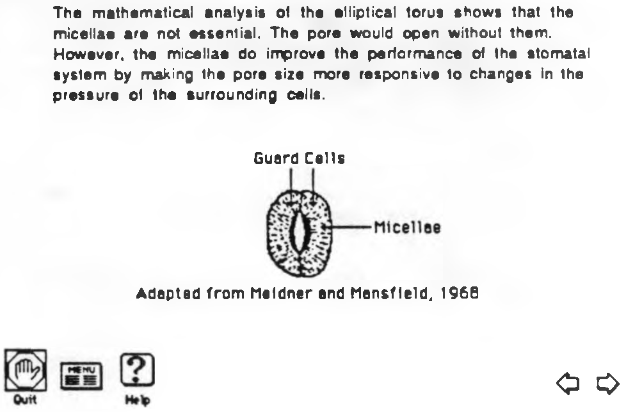


A slightly different view of the guard cell cross section results when the geometric nonlinearity of the shell theory is considered. The pore still opens when the guard cell deformation is perpendicular to the epidermis. However, the outer wall of the guard cell now bulges slightly into the surrounding cell.



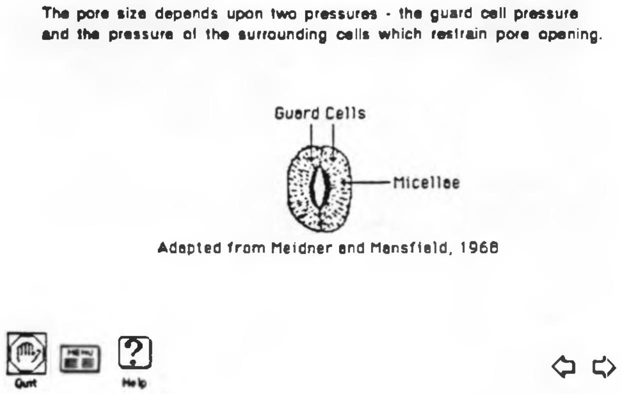
Micellae

The other factor traditionally considered to affect pore size when the guard cell is inflated is the presence inside the guard cell wall of radial fibers, called micellae.



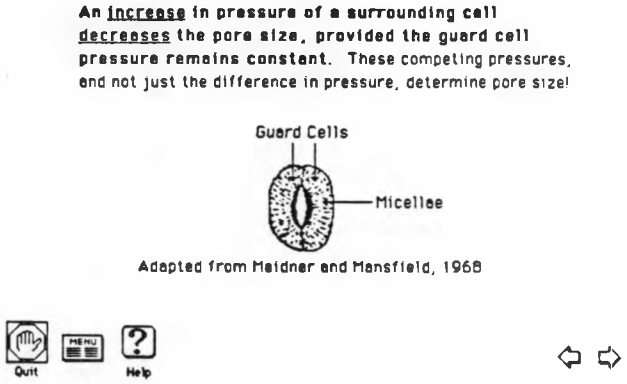
The mathematical analysis of the elliptical torus shows that the micellae are not essential. The pore would open without them. However, the micellae do improve the performance of the stomatal system by making the pore size more responsive to changes in the pressure of the surrounding cells.

Adapted from Meidner and Mansfield, 1968



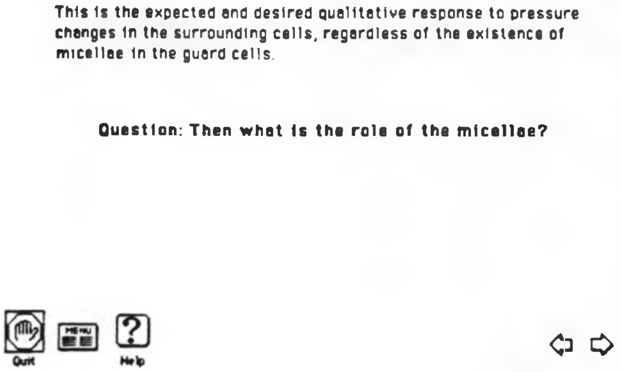
The pore size depends upon two pressures - the guard cell pressure and the pressure of the surrounding cells which restrain pore opening.

Adapted from Meidner and Mansfield, 1968



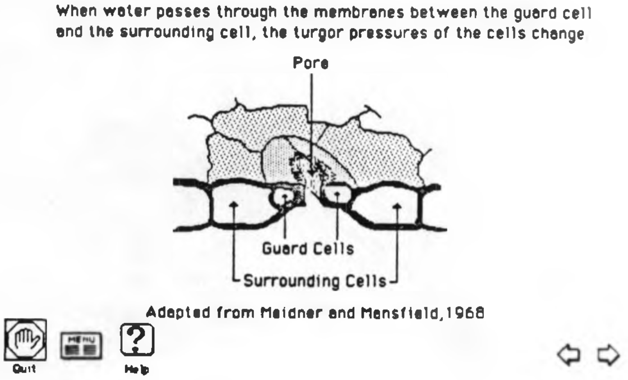
An increase in pressure of a surrounding cell decreases the pore size, provided the guard cell pressure remains constant. These competing pressures, and not just the difference in pressure, determine pore size!

Adapted from Meidner and Mansfield, 1968



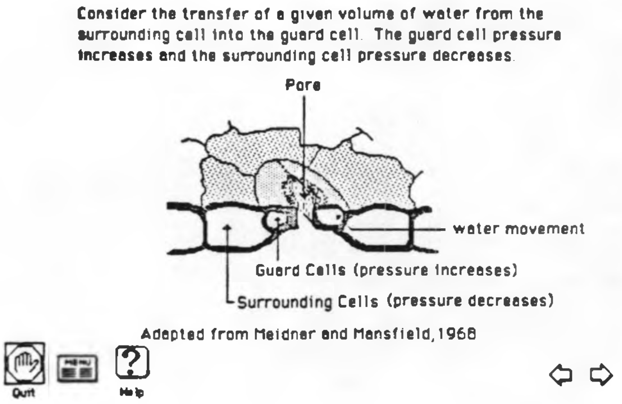
This is the expected and desired qualitative response to pressure changes in the surrounding cells, regardless of the existence of micellae in the guard cells.

Question: Then what is the role of the micellae?



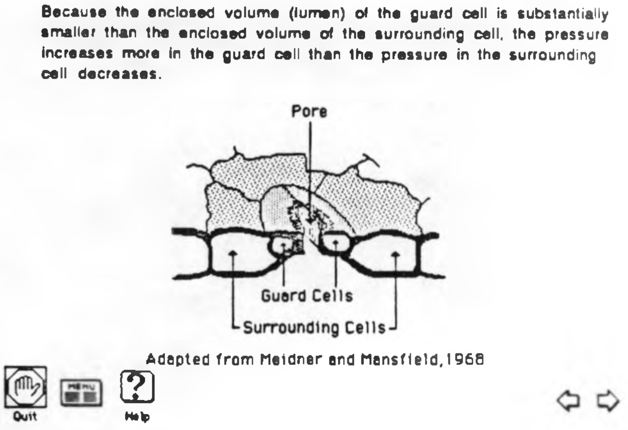
When water passes through the membranes between the guard cell and the surrounding cell, the turgor pressures of the cells change.

Adapted from Meidner and Mansfield,1968



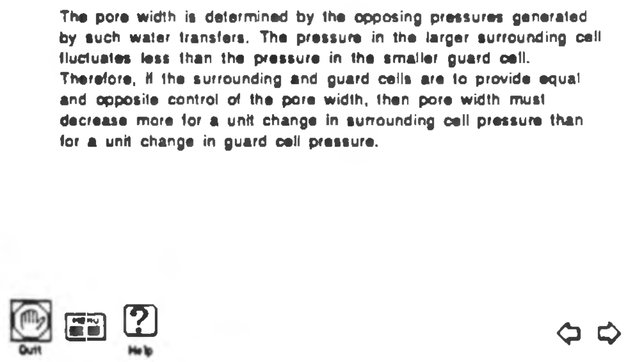
Consider the transfer of a given volume of water from the surrounding cell into the guard cell. The guard cell pressure increases and the surrounding cell pressure decreases.

Adapted from Meidner and Mansfield,1968

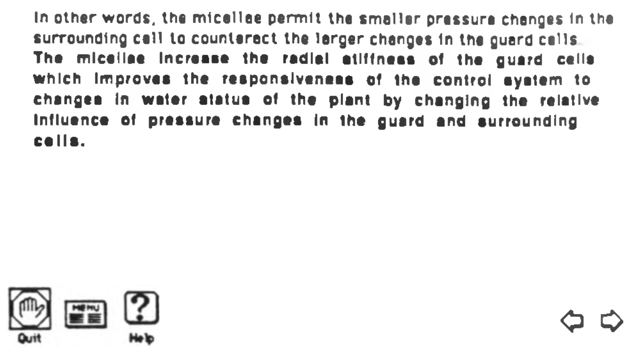


Because the enclosed volume (lumen) of the guard cell is substantially smaller than the enclosed volume of the surrounding cell, the pressure increases more in the guard cell than the pressure in the surrounding cell decreases.

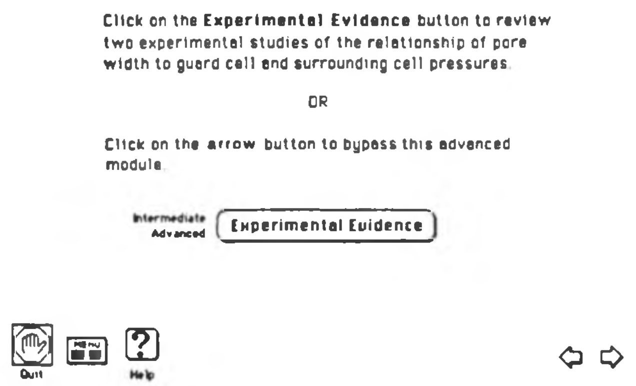
Adapted from Meidner and Mansfield,1968



The pore width is determined by the opposing pressures generated by such water transfers. The pressure in the larger surrounding cell fluctuates less than the pressure in the smaller guard cell. Therefore, if the surrounding and guard cells are to provide equal and opposite control of the pore width, then pore width must decrease more for a unit change in surrounding cell pressure than for a unit change in guard cell pressure.



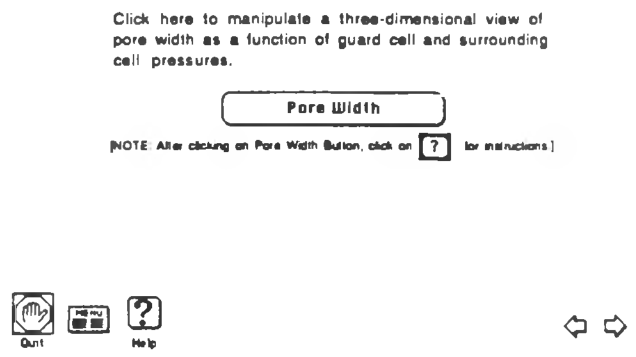
In other words, the micellae permit the smaller pressure changes in the surrounding cell to counteract the larger changes in the guard cells. The micellae increase the radial stiffness of the guard cells which improves the responsiveness of the control system to changes in water status of the plant by changing the relative influence of pressure changes in the guard and surrounding cells.



Click on the **Experimental Evidence** button to review two experimental studies of the relationship of pore width to guard cell and surrounding cell pressures.

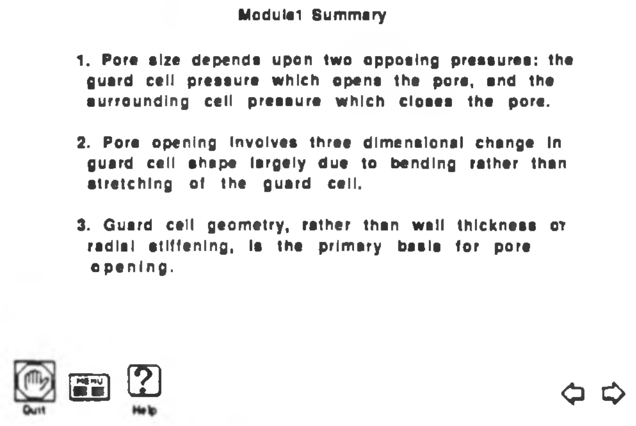
OR

Click on the arrow button to bypass this advanced module.



Click here to manipulate a three-dimensional view of pore width as a function of guard cell and surrounding cell pressures.

[NOTE: After clicking on Pore Width Button, click on ? for instructions.]

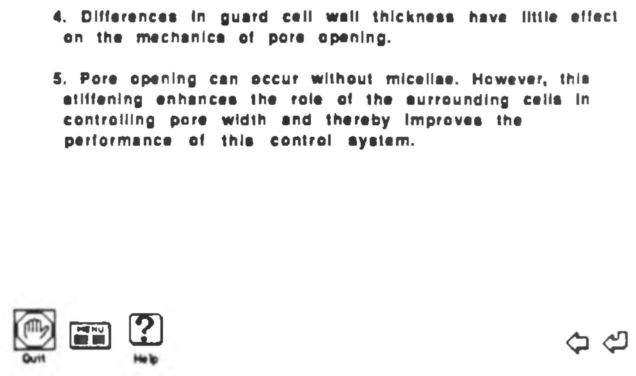


Module1 Summary

1. Pore size depends upon two opposing pressures: the guard cell pressure which opens the pore, and the surrounding cell pressure which closes the pore.

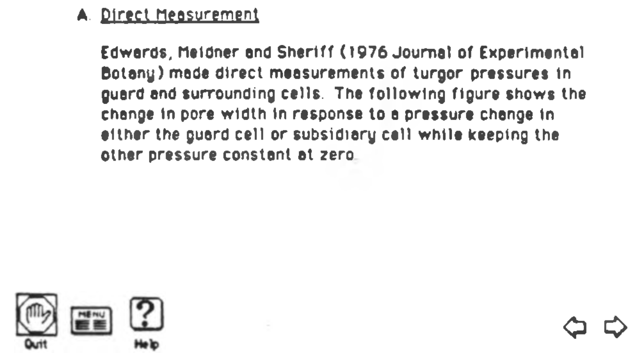
2. Pore opening involves three dimensional change in guard cell shape largely due to bending rather than stretching of the guard cell.

3. Guard cell geometry, rather than wall thickness or radial stiffening, is the primary basis for pore opening.



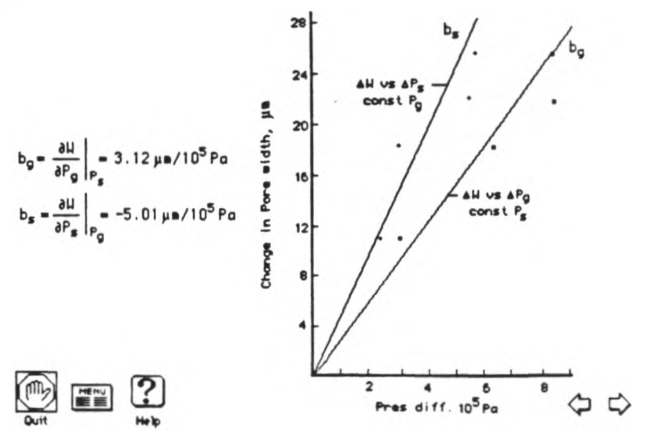
4. Differences in guard cell wall thickness have little effect on the mechanics of pore opening.

5. Pore opening can occur without micellae. However, this stiffening enhances the role of the surrounding cells in controlling pore width and thereby improves the performance of this control system.



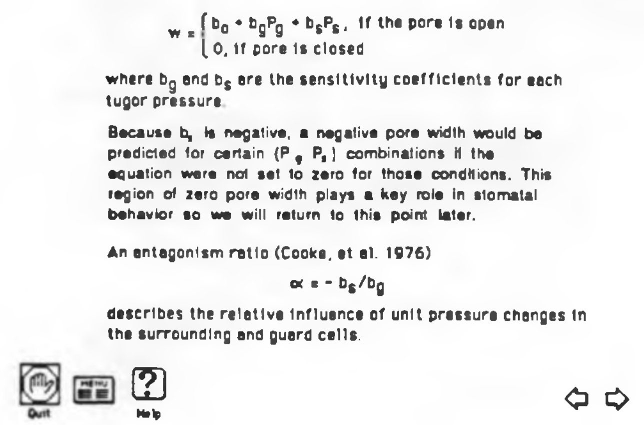
A. Direct Measurement

Edwards, Meidner and Sheriff (1976 Journal of Experimental Botany) made direct measurements of turgor pressures in guard and surrounding cells. The following figure shows the change in pore width in response to a pressure change in either the guard cell or subsidiary cell while keeping the other pressure constant at zero.



$$b_g = \left.\frac{\partial W}{\partial P_g}\right|_{P_s} = 3.12\ \mu m/10^5\ Pa$$

$$b_s = \left.\frac{\partial W}{\partial P_s}\right|_{P_g} = -5.01\ \mu m/10^5\ Pa$$



$$w = \begin{cases} b_0 + b_g P_g + b_s P_s, & \text{if the pore is open} \\ 0, & \text{if pore is closed} \end{cases}$$

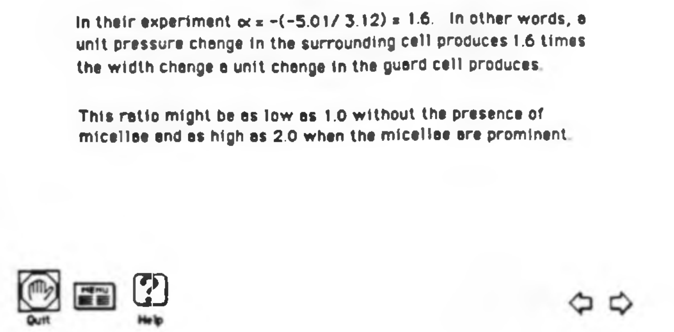
where b_g and b_s are the sensitivity coefficients for each tugor pressure.

Because b_s is negative, a negative pore width would be predicted for certain (P_g, P_s) combinations if the equation were not set to zero for those conditions. This region of zero pore width plays a key role in stomatal behavior so we will return to this point later.

An antagonism ratio (Cooke, et al. 1976)

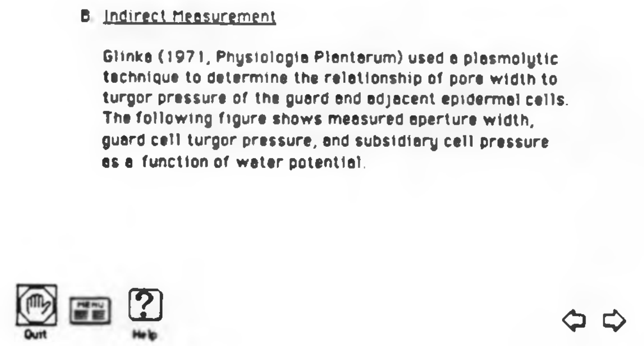
$$\alpha = - b_s / b_g$$

describes the relative influence of unit pressure changes in the surrounding and guard cells.



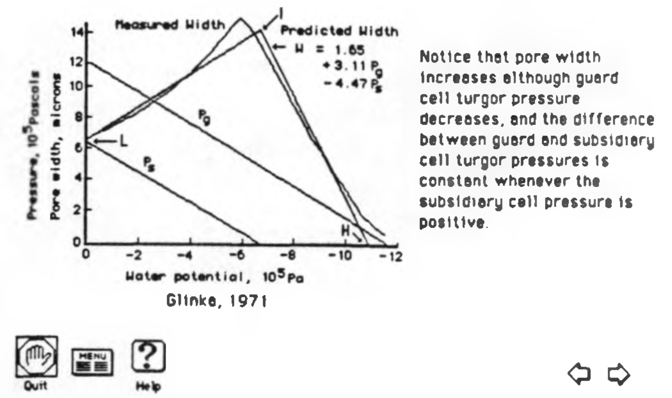
In their experiment $\alpha = -(-5.01 / 3.12) = 1.6$. In other words, a unit pressure change in the surrounding cell produces 1.6 times the width change a unit change in the guard cell produces.

This ratio might be as low as 1.0 without the presence of micellae and as high as 2.0 when the micellae are prominent.



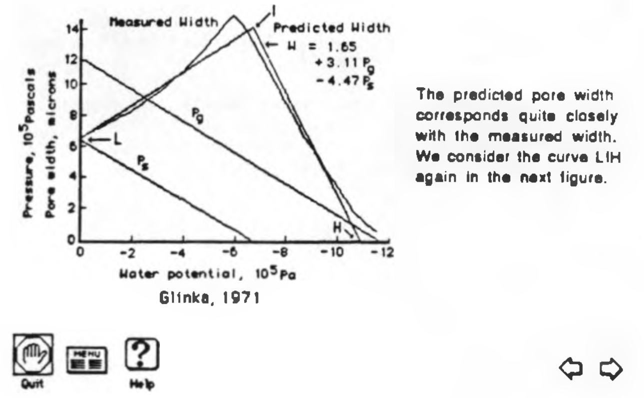
B. Indirect Measurement

Glinka (1971, Physiologia Plantarum) used a plasmolytic technique to determine the relationship of pore width to turgor pressure of the guard and adjacent epidermal cells. The following figure shows measured aperture width, guard cell turgor pressure, and subsidiary cell pressure as a function of water potential.



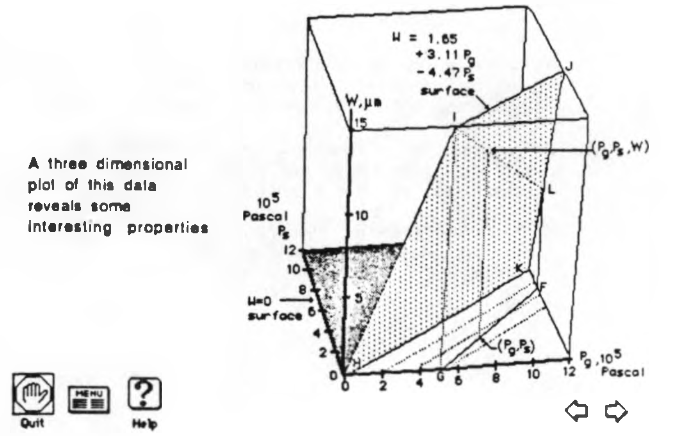
Glinka, 1971

Notice that pore width increases although guard cell turgor pressure decreases, and the difference between guard and subsidiary cell turgor pressures is constant whenever the subsidiary cell pressure is positive.

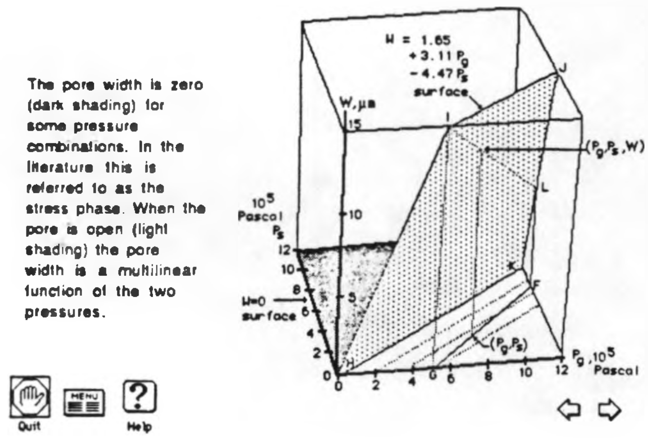


Glinka, 1971

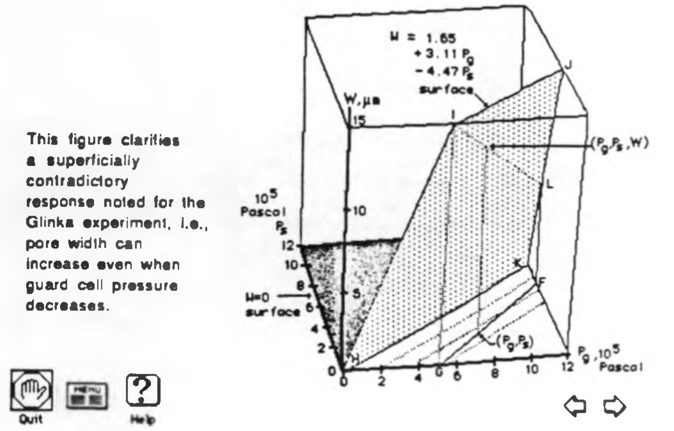
The predicted pore width corresponds quite closely with the measured width. We consider the curve LIH again in the next figure.



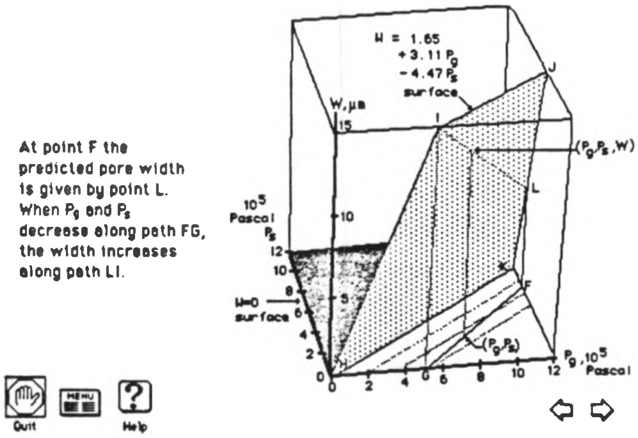
A three dimensional plot of this data reveals some interesting properties



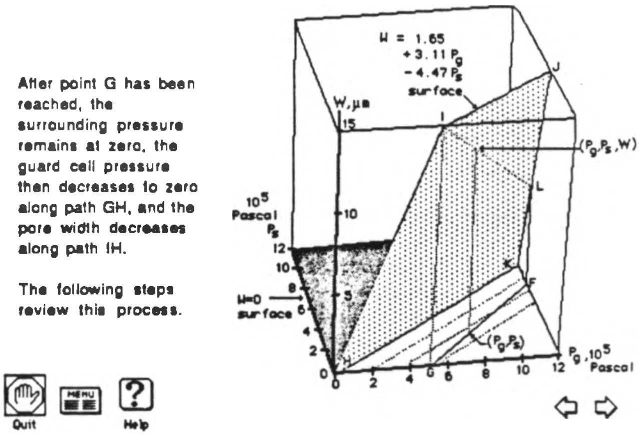
The pore width is zero (dark shading) for some pressure combinations. In the literature this is referred to as the stress phase. When the pore is open (light shading) the pore width is a multilinear function of the two pressures.



This figure clarifies a superficially contradictory response noted for the Glinka experiment, i.e., pore width can increase even when guard cell pressure decreases.

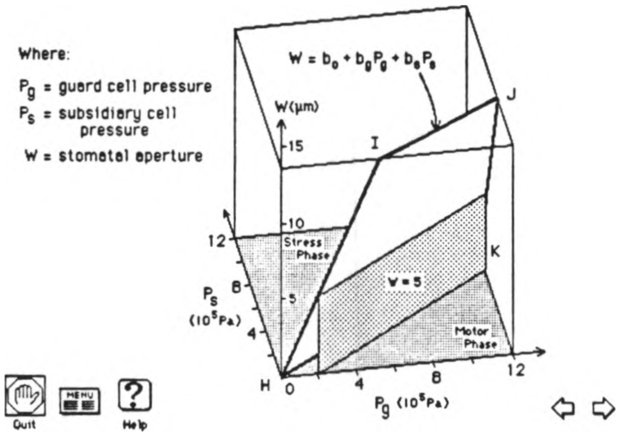


At point F the predicted pore width is given by point L. When P_g and P_s decrease along path FG, the width increases along path LI.



After point G has been reached, the surrounding pressure remains at zero, the guard cell pressure then decreases to zero along path GH, and the pore width decreases along path IH.

The following steps review this process.

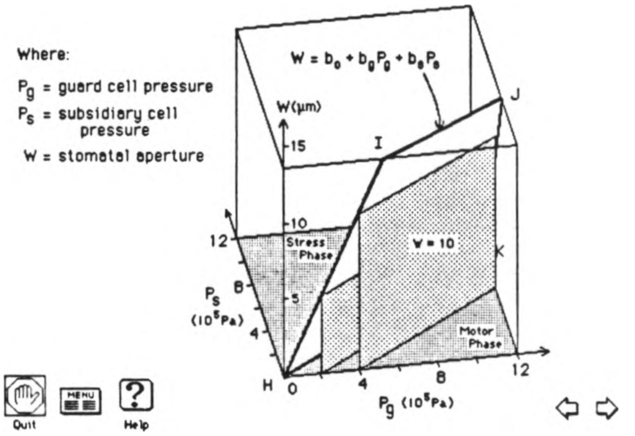


Where:

P_g = guard cell pressure

P_s = subsidiary cell pressure

W = stomatal aperture

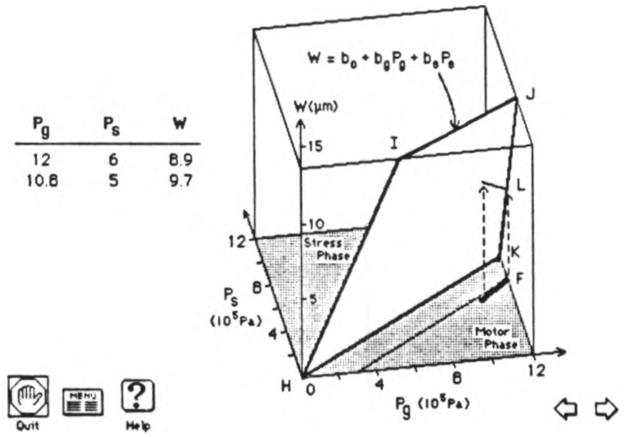


Where:

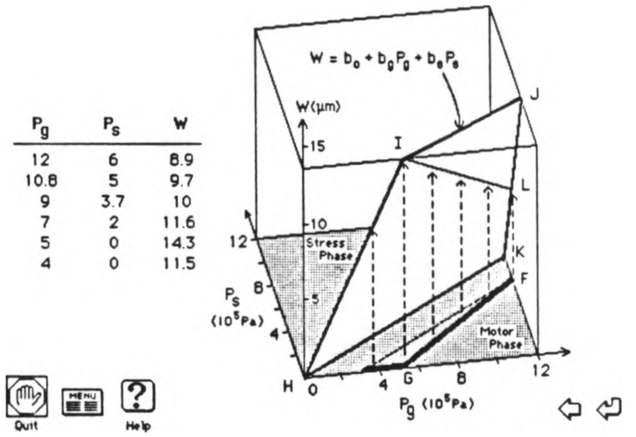
P_g = guard cell pressure

P_s = subsidiary cell pressure

W = stomatal aperture



P_g	P_s	W
12	6	8.9
10.8	5	9.7



P_g	P_s	W
12	6	8.9
10.8	5	9.7
9	3.7	10
7	2	11.6
5	0	14.3
4	0	11.5

Module 2 Pore Size Affects Diffusion Rate

In addition to capturing sunlight required for photosynthesis, the leaf structure also facilitates the exchange of gases. The width-adjustable pores described in Module I control the exchange of gases between the leaf interior and the atmosphere. Gas exchange through the stomates occurs by diffusion from a region of higher concentration to a region of lower concentration.

Quit MENU Help

Since the overall rate of diffusion also depends upon the pathway and its dimensions, changes in pore width affect the rate of exchange. As you shall see in a moment, **the leaf has a design which facilitates a surprisingly high rate of exchange of water vapor, carbon dioxide, and oxygen.**

Quit MENU Help

Remember that both carbon dioxide and water vapor diffuse through the stomatal pore, but in opposite directions. In this module we discuss only **the diffusion of water vapor and relate pore width to the rate of diffusion**. However, the discussion applies equally to the carbon dioxide pathway.

This design assures a plentiful supply of carbon dioxide for use in photosynthesis, but at the same time creates a large demand for water. The plant adjusts stomatal pore width to mediate these conflicting processes. This module deals with the stomate as the controlling valve in that process.

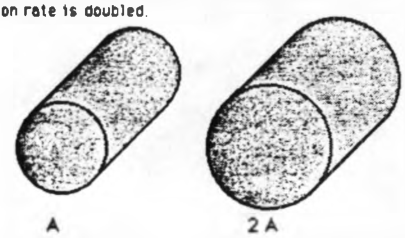
Quit MENU Help

The diffusion rate of water vapor from a leaf can approach 90% of the rate of evaporation from an open surface of water the same size as the leaf! This occurs even though the open pores constitute no more than 2% of the leaf surface. This capacity for water loss accounts for the expensive process of irrigation used in commercial agriculture.

Question: What is the mechanism used to achieve this high level of effectiveness?

Quit MENU Help

Again, geometry provides the clue. Consider the case of diffusion of water vapor through a circular pipe where water vapor at each end of the pipe is maintained at a different concentration. The diffusion rate in this case is proportional to the cross sectional area of the pipe. If the cross sectional area is doubled, the diffusion rate is doubled.

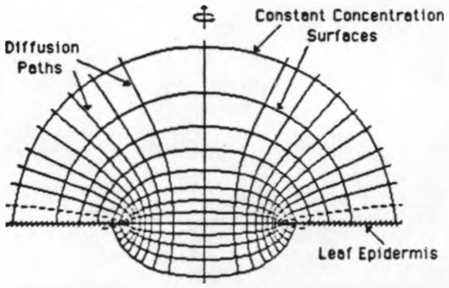


Double cross-sectional area to double diffusion rate

Quit MENU Help

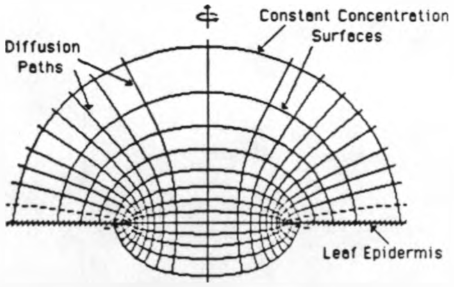
Question: The diffusion rate for stomates is not proportional to the pore area. Why?

Quit MENU Help



The above schematic representation of the cross section of a leaf suggests the answer. The lines passing through the pore depict the pathway for diffusion at various points within the pore. The diffusion paths are perpendicular to these equal concentration surfaces which form a family of oblate spheroids in this case.

Quit MENU Help



The equal concentration surfaces are just a three dimensional generalization of constant pressure lines on a weather map. At the middle of a pore the diffusion occurs in a straight line; therefore, that portion of the path resembles the pipe example mentioned before.

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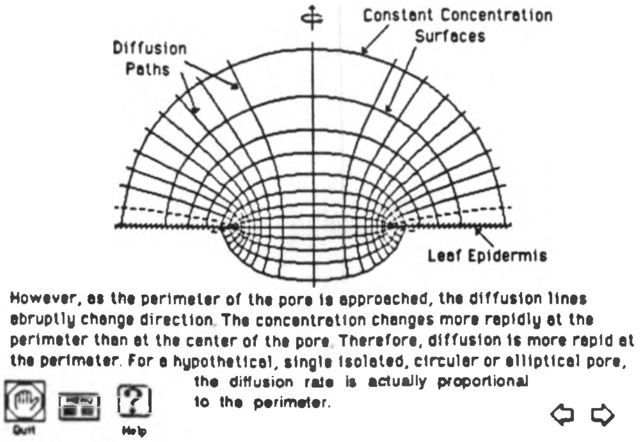
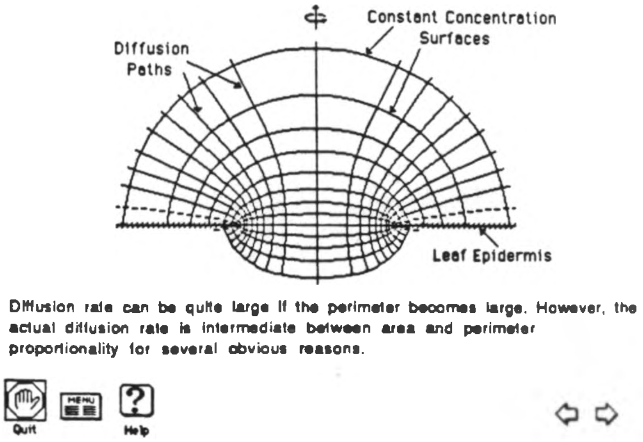
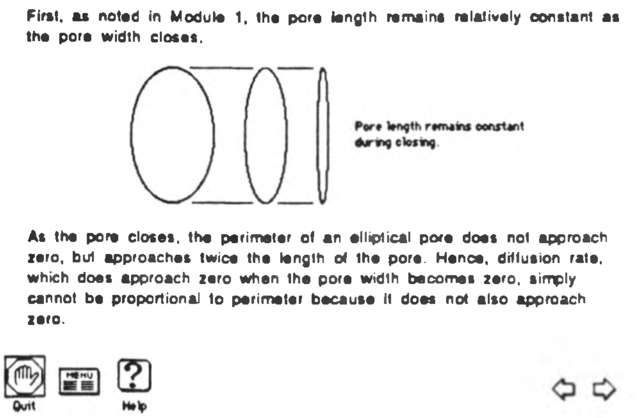


However, as the perimeter of the pore is approached, the diffusion lines abruptly change direction. The concentration changes more rapidly at the perimeter than at the center of the pore. Therefore, diffusion is more rapid at the perimeter. For a hypothetical, single isolated, circular or elliptical pore, the diffusion rate is actually proportional to the perimeter.

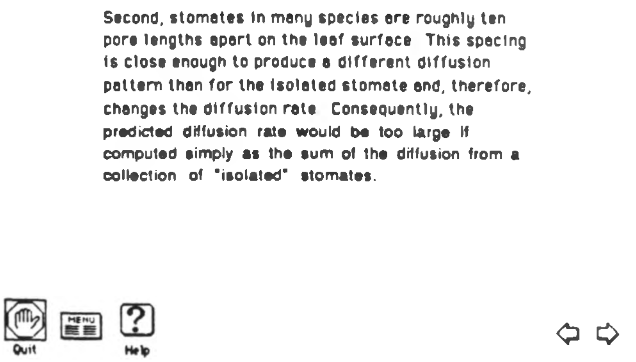


Diffusion rate can be quite large if the perimeter becomes large. However, the actual diffusion rate is intermediate between area and perimeter proportionality for several obvious reasons.

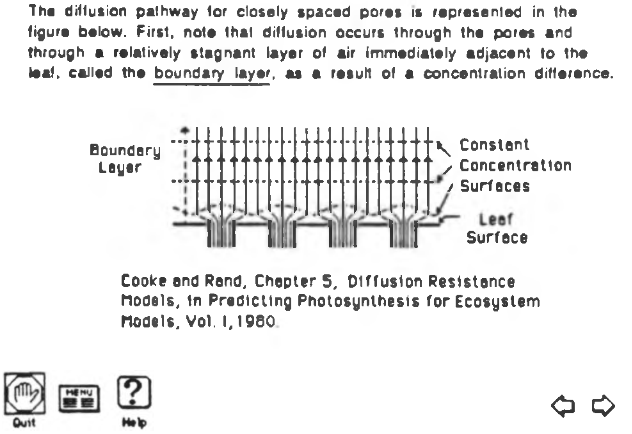


First, as noted in Module 1, the pore length remains relatively constant as the pore width closes.

As the pore closes, the perimeter of an elliptical pore does not approach zero, but approaches twice the length of the pore. Hence, diffusion rate, which does approach zero when the pore width becomes zero, simply cannot be proportional to perimeter because it does not also approach zero.

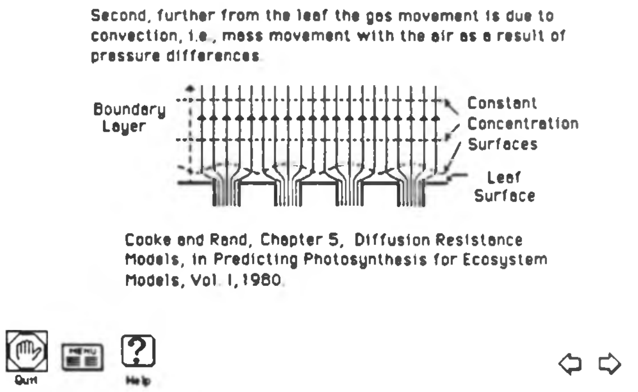


Second, stomates in many species are roughly ten pore lengths apart on the leaf surface. This spacing is close enough to produce a different diffusion pattern than for the isolated stomate and, therefore, changes the diffusion rate. Consequently, the predicted diffusion rate would be too large if computed simply as the sum of the diffusion from a collection of "isolated" stomates.



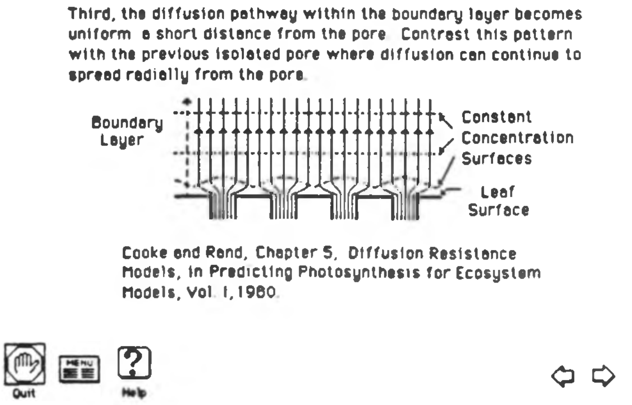
The diffusion pathway for closely spaced pores is represented in the figure below. First, note that diffusion occurs through the pores and through a relatively stagnant layer of air immediately adjacent to the leaf, called the boundary layer, as a result of a concentration difference.

Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol. I, 1980.



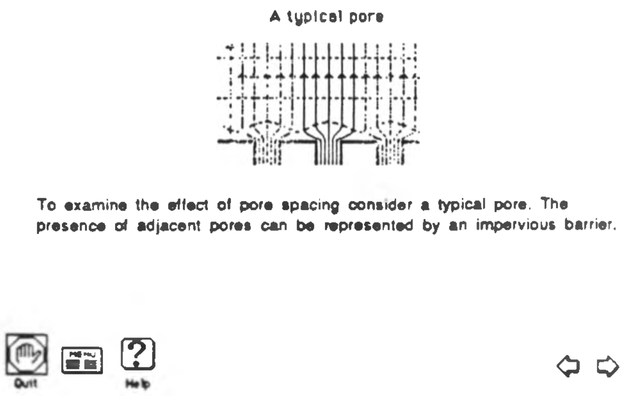
Second, further from the leaf the gas movement is due to convection, i.e., mass movement with the air as a result of pressure differences.

Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol. I, 1980.



Third, the diffusion pathway within the boundary layer becomes uniform a short distance from the pore. Contrast this pattern with the previous isolated pore where diffusion can continue to spread radially from the pore.

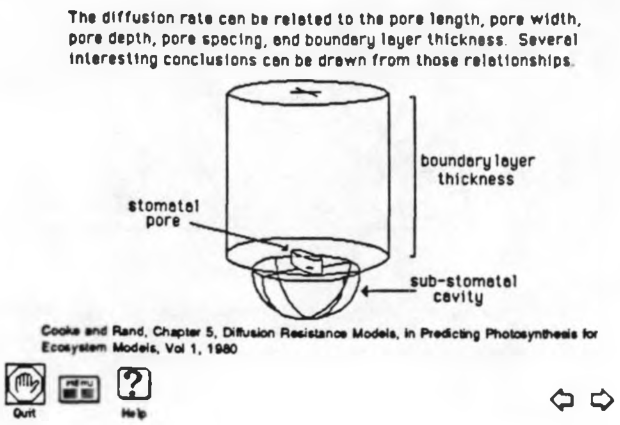
Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol. I, 1980.



A typical pore

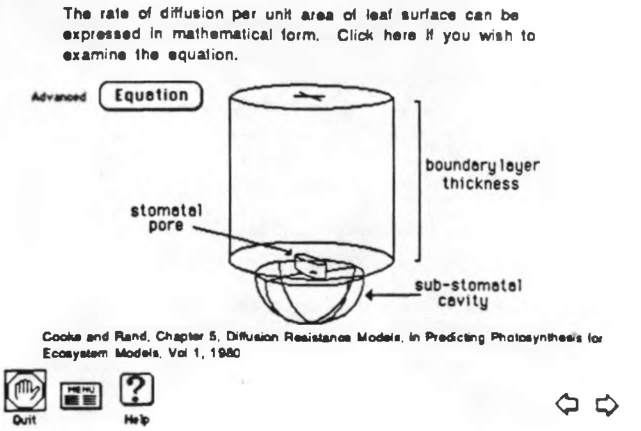
To examine the effect of pore spacing consider a typical pore. The presence of adjacent pores can be represented by an impervious barrier.

Stomate2 p 2-3



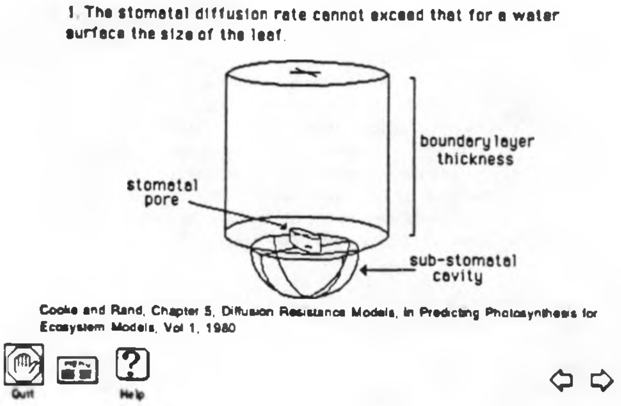
The diffusion rate can be related to the pore length, pore width, pore depth, pore spacing, and boundary layer thickness. Several interesting conclusions can be drawn from those relationships.

Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol 1, 1980



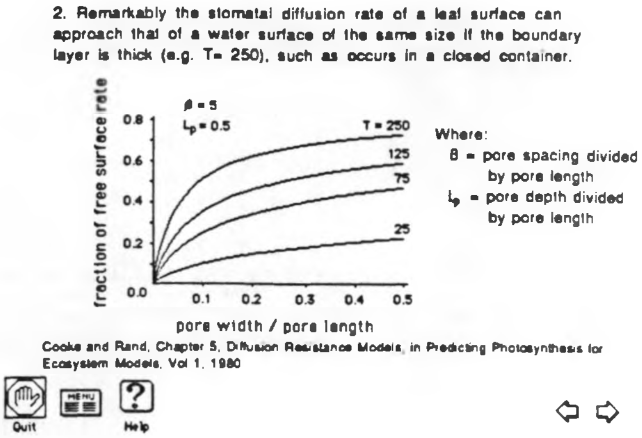
The rate of diffusion per unit area of leaf surface can be expressed in mathematical form. Click here if you wish to examine the equation.

Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol 1, 1980



1. The stomatal diffusion rate cannot exceed that for a water surface the size of the leaf.

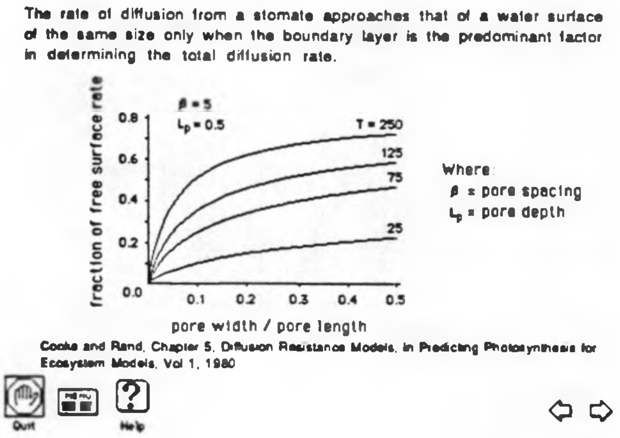
Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol 1, 1980



2. Remarkably the stomatal diffusion rate of a leaf surface can approach that of a water surface of the same size if the boundary layer is thick (e.g. T= 250), such as occurs in a closed container.

Where:
β = pore spacing divided by pore length
L_p = pore depth divided by pore length

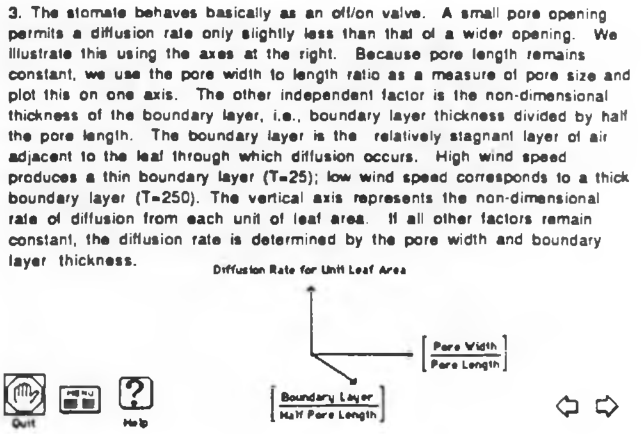
Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol 1, 1980



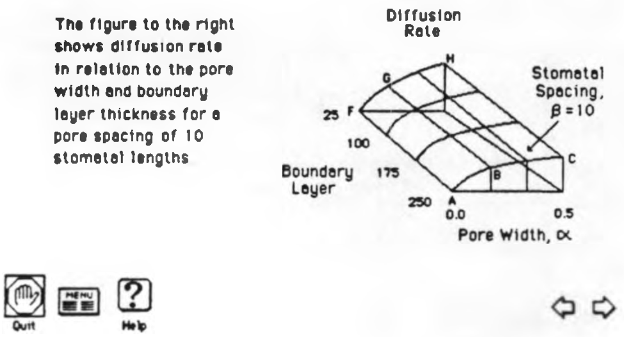
The rate of diffusion from a stomate approaches that of a water surface of the same size only when the boundary layer is the predominant factor in determining the total diffusion rate.

Where:
β = pore spacing
L_p = pore depth

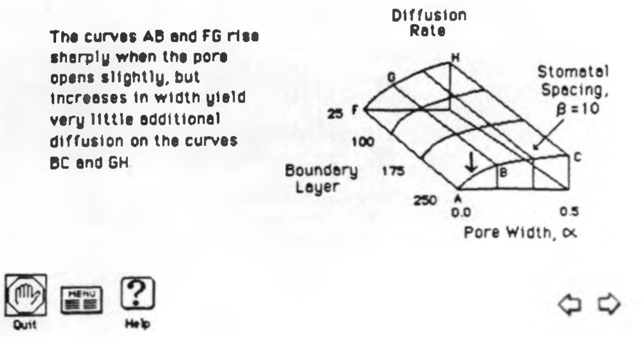
Cooke and Rand, Chapter 5, Diffusion Resistance Models, in Predicting Photosynthesis for Ecosystem Models, Vol 1, 1980



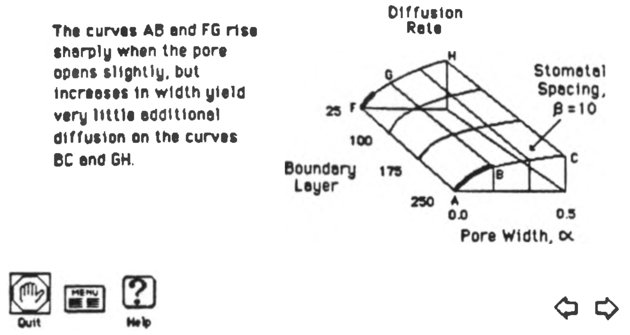
3. The stomate behaves basically as an off/on valve. A small pore opening permits a diffusion rate only slightly less than that of a wider opening. We illustrate this using the axes at the right. Because pore length remains constant, we use the pore width to length ratio as a measure of pore size and plot this on one axis. The other independent factor is the non-dimensional thickness of the boundary layer, i.e., boundary layer thickness divided by half the pore length. The boundary layer is the relatively stagnant layer of air adjacent to the leaf through which diffusion occurs. High wind speed produces a thin boundary layer (T=25); low wind speed corresponds to a thick boundary layer (T=250). The vertical axis represents the non-dimensional rate of diffusion from each unit of leaf area. If all other factors remain constant, the diffusion rate is determined by the pore width and boundary layer thickness.



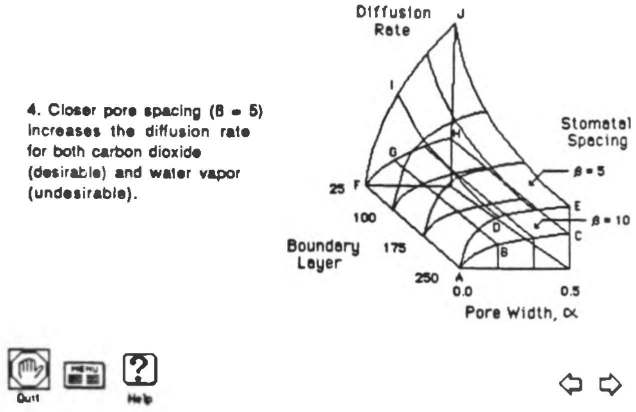
The figure to the right shows diffusion rate in relation to the pore width and boundary layer thickness for a pore spacing of 10 stomatal lengths



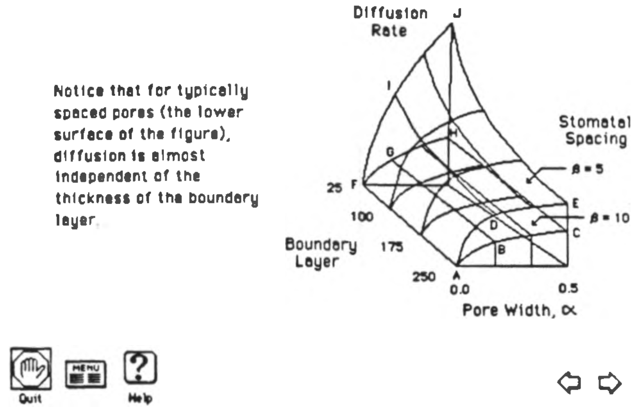
The curves AB and FG rise sharply when the pore opens slightly, but increases in width yield very little additional diffusion on the curves BC and GH.



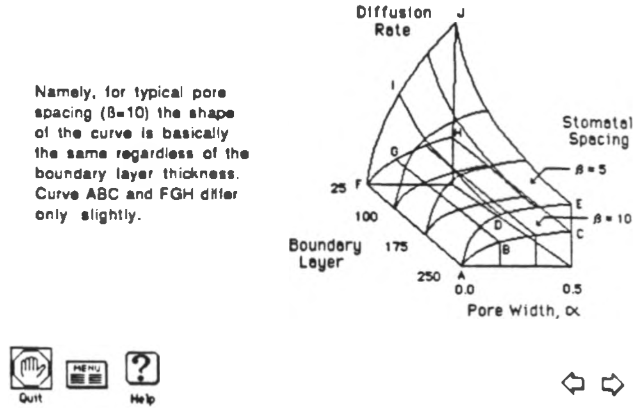
The curves AB and FG rise sharply when the pore opens slightly, but increases in width yield very little additional diffusion on the curves BC and GH.



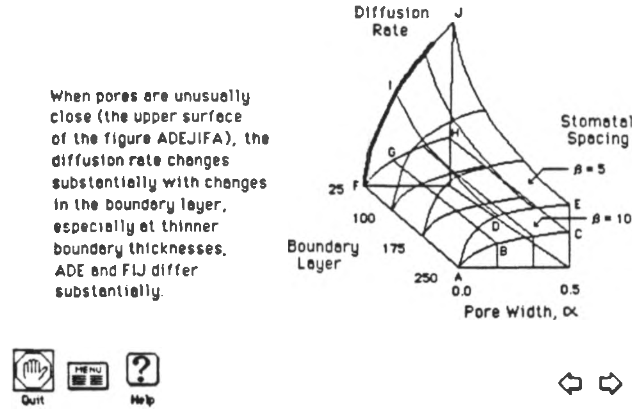
4. Closer pore spacing (β = 5) increases the diffusion rate for both carbon dioxide (desirable) and water vapor (undesirable).



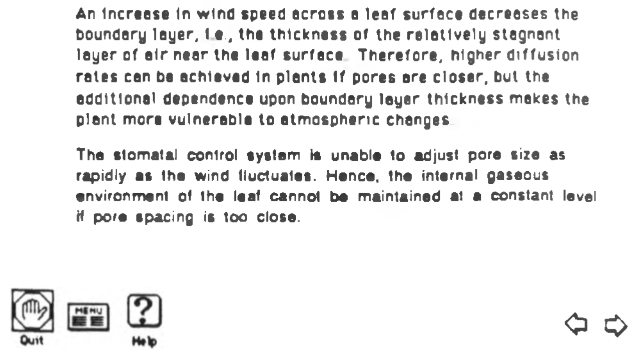
Notice that for typically spaced pores (the lower surface of the figure), diffusion is almost independent of the thickness of the boundary layer.



Namely, for typical pore spacing (β=10) the shape of the curve is basically the same regardless of the boundary layer thickness. Curve ABC and FGH differ only slightly.

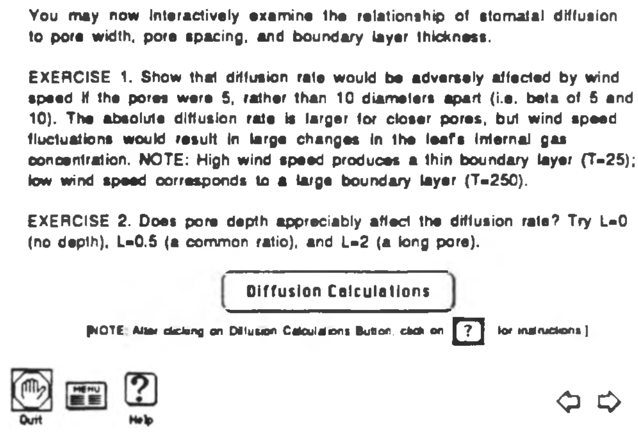


When pores are unusually close (the upper surface of the figure ADEJIFA), the diffusion rate changes substantially with changes in the boundary layer, especially at thinner boundary thicknesses. ADE and FIJ differ substantially.



An increase in wind speed across a leaf surface decreases the boundary layer, i.e., the thickness of the relatively stagnant layer of air near the leaf surface. Therefore, higher diffusion rates can be achieved in plants if pores are closer, but the additional dependence upon boundary layer thickness makes the plant more vulnerable to atmospheric changes.

The stomatal control system is unable to adjust pore size as rapidly as the wind fluctuates. Hence, the internal gaseous environment of the leaf cannot be maintained at a constant level if pore spacing is too close.

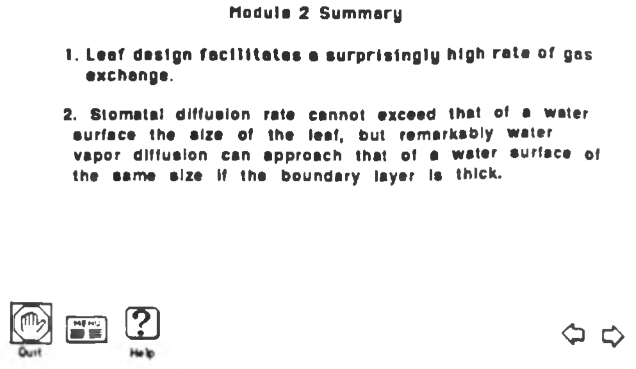


You may now interactively examine the relationship of stomatal diffusion to pore width, pore spacing, and boundary layer thickness.

EXERCISE 1. Show that diffusion rate would be adversely affected by wind speed if the pores were 5, rather than 10 diameters apart (i.e. beta of 5 and 10). The absolute diffusion rate is larger for closer pores, but wind speed fluctuations would result in large changes in the leafs internal gas concentration. NOTE: High wind speed produces a thin boundary layer (T=25); low wind speed corresponds to a large boundary layer (T=250).

EXERCISE 2. Does pore depth appreciably affect the diffusion rate? Try L=0 (no depth), L=0.5 (a common ratio), and L=2 (a long pore).

[NOTE: After clicking on Diffusion Calculations Button, click on ? for instructions.]



Module 2 Summary

1. Leaf design facilitates a surprisingly high rate of gas exchange.

2. Stomatal diffusion rate cannot exceed that of a water surface the size of the leaf, but remarkably water vapor diffusion can approach that of a water surface of the same size if the boundary layer is thick.

3. **Stomatal diffusion rate is intermediate between area and perimeter proportionality.**

4. **The stomate behaves basically as an on-off valve.**

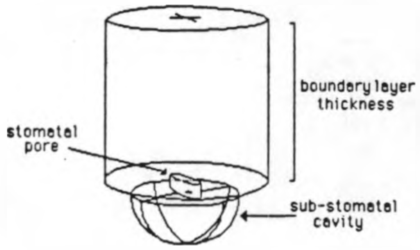
5. **Closer than normal pore spacing increases the diffusion rate but causes an undesirable dependence on wind speed. The typical pore spacing of ten diameters permits the highest diffusion rate without introducing wind speed dependence.**

Quit Help ⇦ ⏎

When two physical systems are governed by the same equations and one is easier to measure than the other, relationships discovered using one can be applied to the other. In this instance, electrical measurements can be made more easily on an electrolytic tank analog of the stomatal diffusion problem. These measurements are proportional to the corresponding diffusion measurements.

Quit Help ⇦ ⇨

Holcomb and Cooke (1977) used this technique to develop the following empirical relationship for diffusion per unit leaf area J as a function of pore geometry, pore spacing and boundary layer thickness:



Quit Help ⇦ ⇨

$$\boxed{J = \Delta C\,(D/A) \,/\, [T + L_p\beta^2/\alpha + \beta^2 \ln(4/\alpha) - \beta]}$$

where

J = diffusion per unit leaf area, gm/cm^2 s

ΔC = gas concentration difference between bottom of the stomatal cavity and the atmosphere, gm/cm^3

D = diffusion coefficient, cm^2/s

a = pore half length, cm

b = pore half width, cm

d = pore depth, cm

l_c = thickness of boundary layer on leaf surface, cm

N = number of stomates per cm^2

$\alpha = b/a$ width to length aspect ratio of pore, $0.05 <= \alpha <= 0.5$

$\beta = (\pi N)^{-1/2}/a, \quad \beta >= 2$

T = nondimensional boundary layer thickness, $= l_c/a >= \beta >= 2$

L_p = nondimensional pore depth $= d/a >= 0$

Quit Help ⇦ ⇨

Typical values:

$0.025 <= l_c <= 0.25$ cm

$a = 10^{-3}$ cm

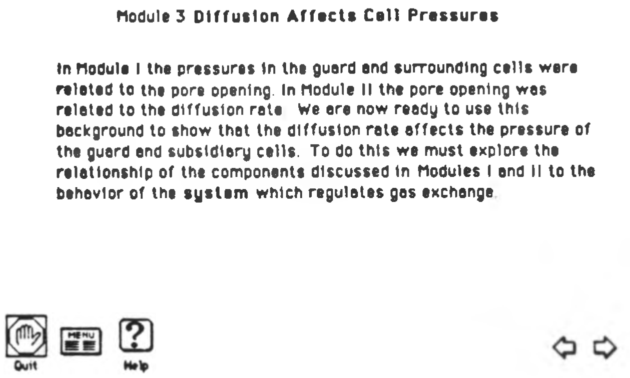
$L = 0.5$

Relationships become clearer if the diffusion expression is written completely in non-dimensional form for conductance.

$$\boxed{\left[\frac{J}{\Delta C\,(D/a)}\right] = [T + L_p\beta^2/\alpha + \beta^2 \ln(4/\alpha) - \beta]^{-1}}$$

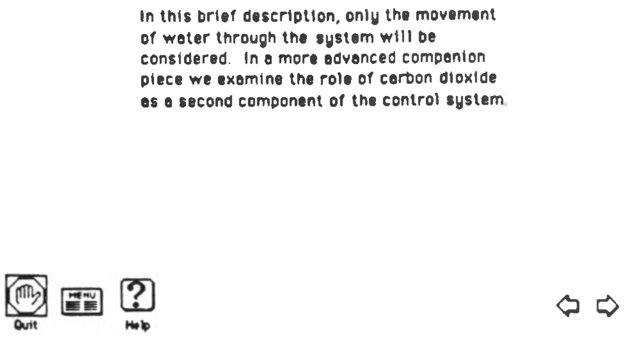
This expression relates J to concentration difference, diffusion coefficient, pore half length, nondimensional boundary layer thickness, nondimensional pore depth, nondimensional pore spacing, and nondimensional pore width.

Quit Help ⇦ ⏎

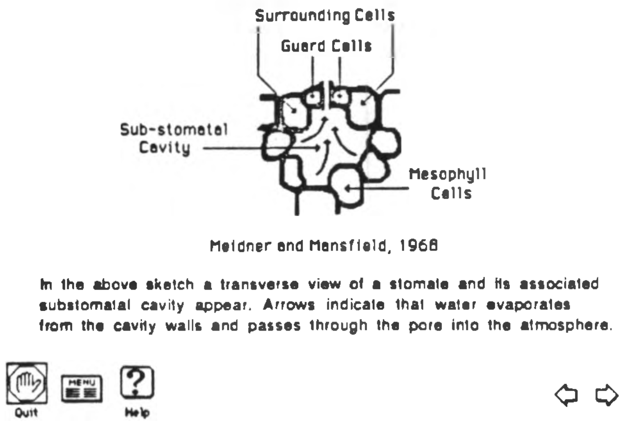


Module 3 Diffusion Affects Cell Pressures

In Module I the pressures in the guard and surrounding cells were related to the pore opening. In Module II the pore opening was related to the diffusion rate. We are now ready to use this background to show that the diffusion rate affects the pressure of the guard and subsidiary cells. To do this we must explore the relationship of the components discussed in Modules I and II to the behavior of the system which regulates gas exchange.

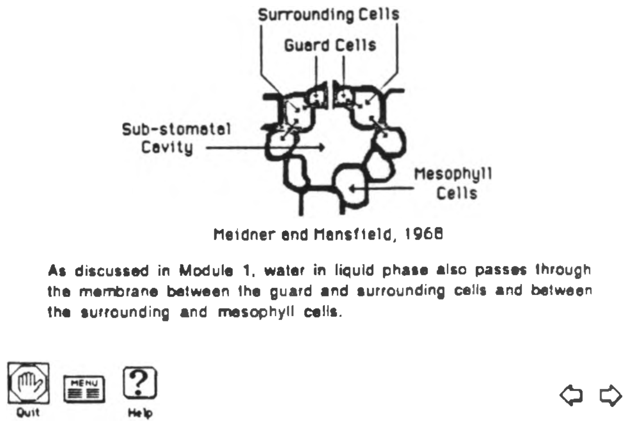


In this brief description, only the movement of water through the system will be considered. In a more advanced companion piece we examine the role of carbon dioxide as a second component of the control system.



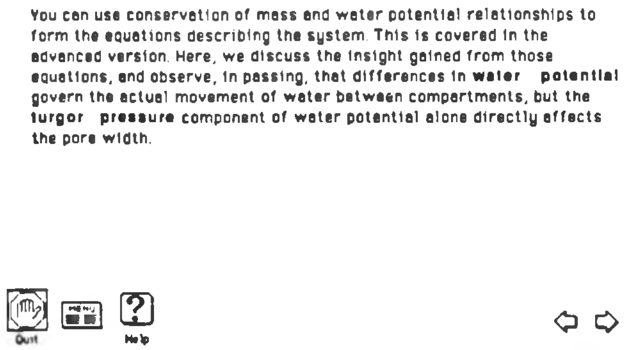
Meidner and Mansfield, 1968

In the above sketch a transverse view of a stomate and its associated substomatal cavity appear. Arrows indicate that water evaporates from the cavity walls and passes through the pore into the atmosphere.

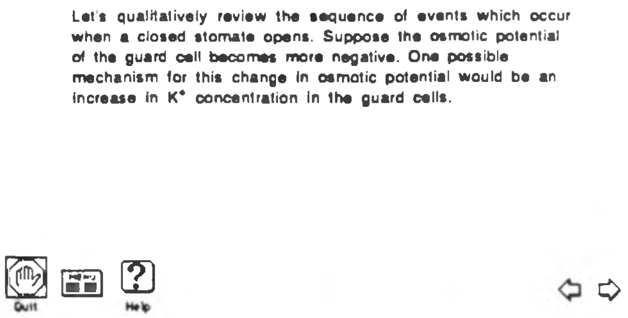


Meidner and Mansfield, 1968

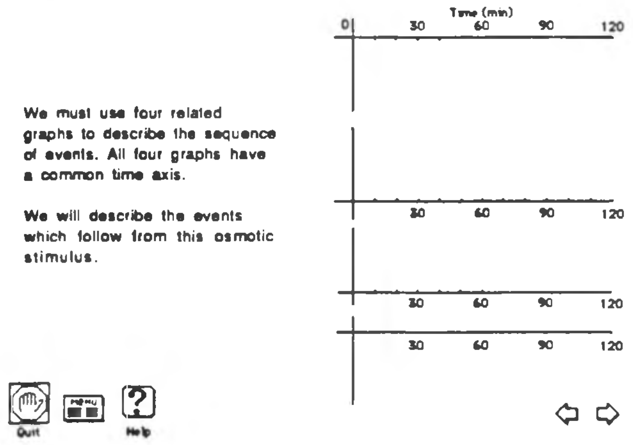
As discussed in Module 1, water in liquid phase also passes through the membrane between the guard and surrounding cells and between the surrounding and mesophyll cells.



You can use conservation of mass and water potential relationships to form the equations describing the system. This is covered in the advanced version. Here, we discuss the insight gained from those equations, and observe, in passing, that differences in **water potential** govern the actual movement of water between compartments, but the **turgor pressure** component of water potential alone directly affects the pore width.

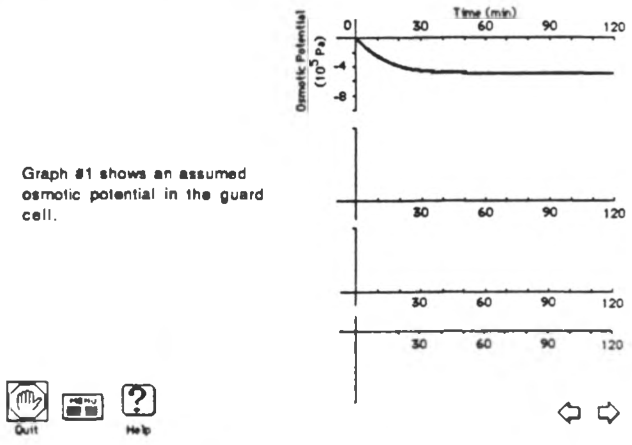


Let's qualitatively review the sequence of events which occur when a closed stomate opens. Suppose the osmotic potential of the guard cell becomes more negative. One possible mechanism for this change in osmotic potential would be an increase in K^+ concentration in the guard cells.

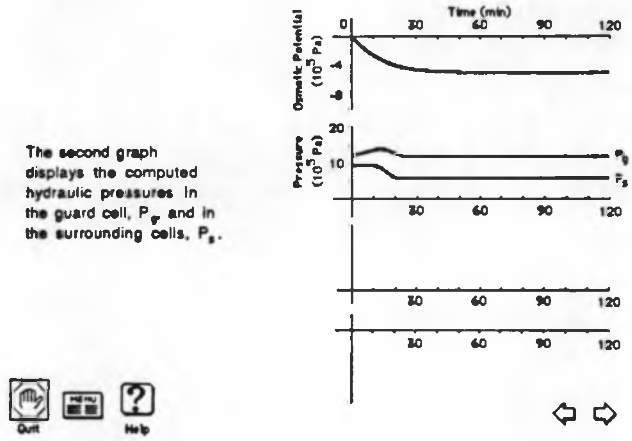


We must use four related graphs to describe the sequence of events. All four graphs have a common time axis.

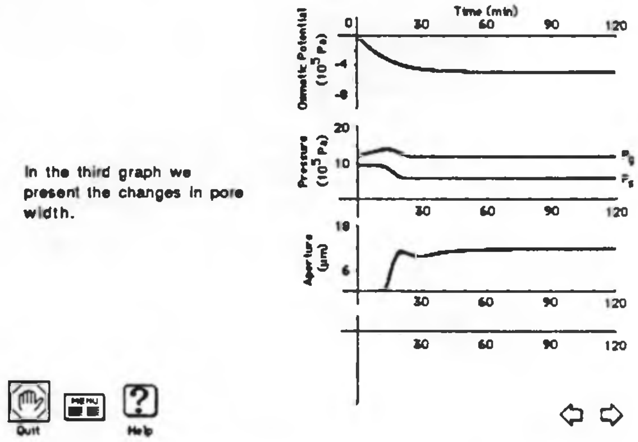
We will describe the events which follow from this osmotic stimulus.



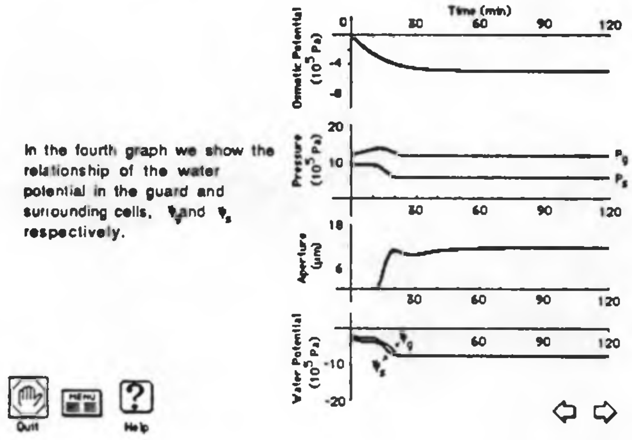
Graph #1 shows an assumed osmotic potential in the guard cell.



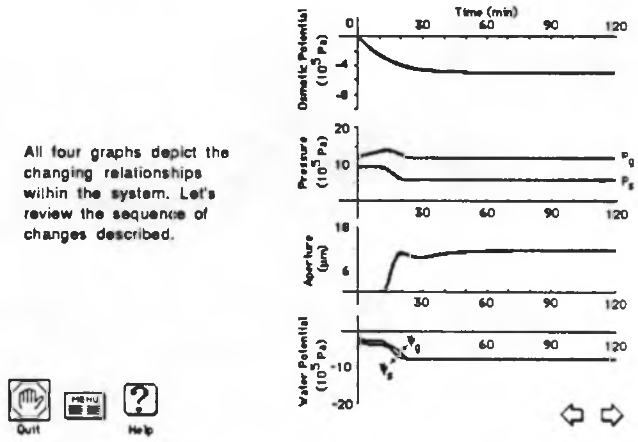
The second graph displays the computed hydraulic pressures in the guard cell, P_g, and in the surrounding cells, P_s.



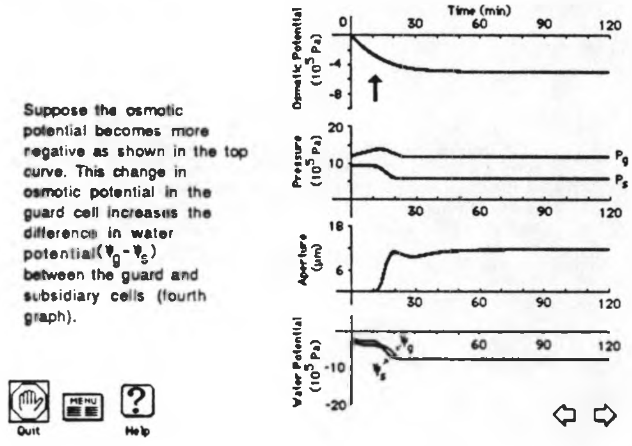
In the third graph we present the changes in pore width.



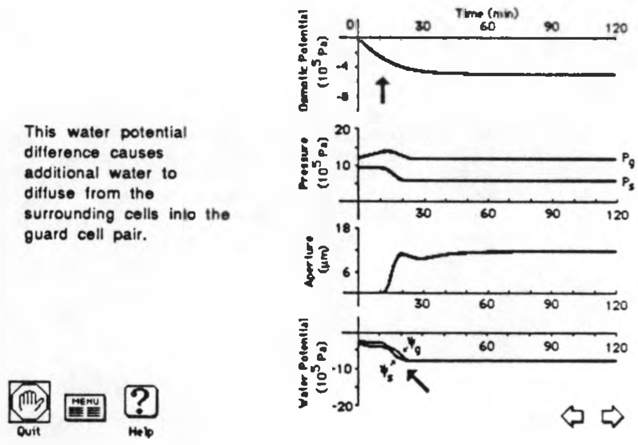
In the fourth graph we show the relationship of the water potential in the guard and surrounding cells, Ψ_g and Ψ_s respectively.



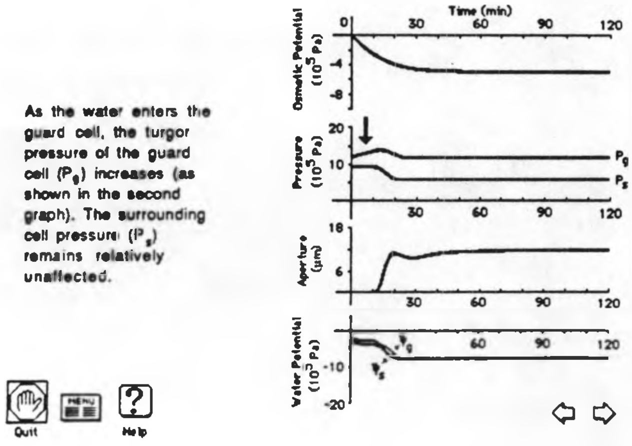
All four graphs depict the changing relationships within the system. Let's review the sequence of changes described.



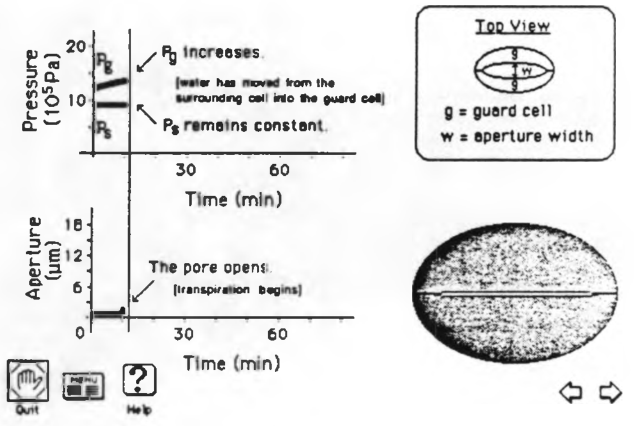
Suppose the osmotic potential becomes more negative as shown in the top curve. This change in osmotic potential in the guard cell increases the difference in water potential($\Psi_g - \Psi_s$) between the guard and subsidiary cells (fourth graph).

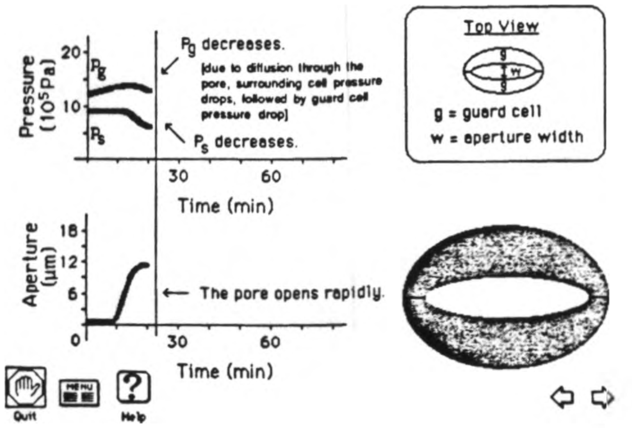


This water potential difference causes additional water to diffuse from the surrounding cells into the guard cell pair.



As the water enters the guard cell, the turgor pressure of the guard cell (P_g) increases (as shown in the second graph). The surrounding cell pressure (P_s) remains relatively unaffected.





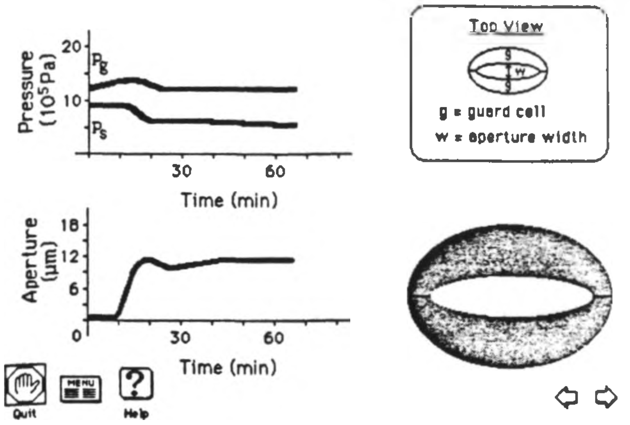
P_g decreases.

[due to diffusion through the pore, surrounding cell pressure drops, followed by guard cell pressure drop]

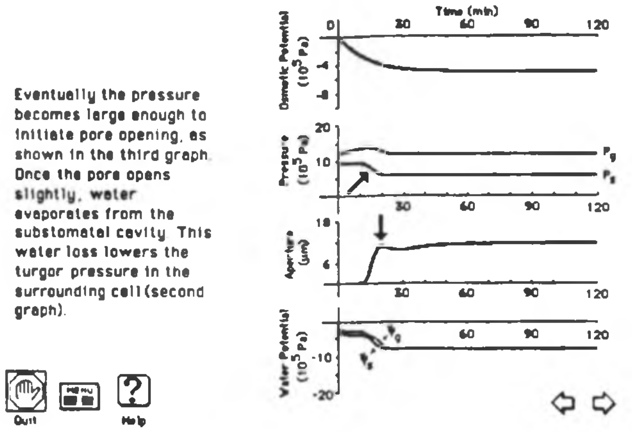
P_s decreases.

← The pore opens rapidly.

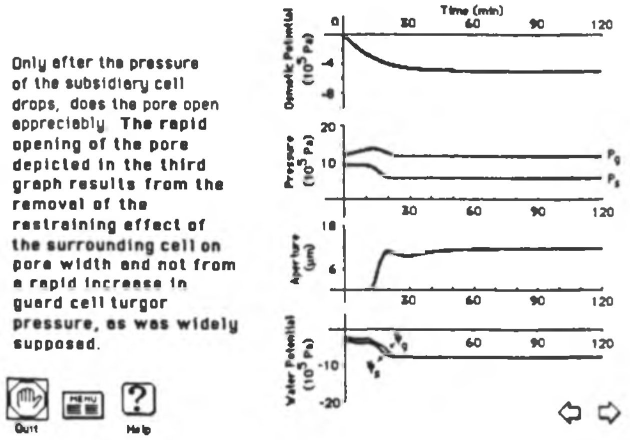
g = guard cell
w = aperture width



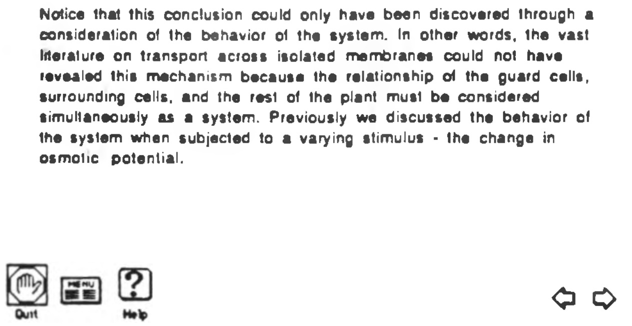
g = guard cell
w = aperture width



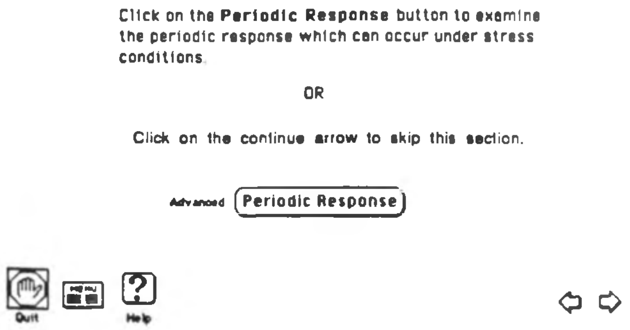
Eventually the pressure becomes large enough to initiate pore opening, as shown in the third graph. Once the pore opens slightly, water evaporates from the substomatal cavity. This water loss lowers the turgor pressure in the surrounding cell (second graph).



Only after the pressure of the subsidiary cell drops, does the pore open appreciably. The rapid opening of the pore depicted in the third graph results from the removal of the restraining effect of the surrounding cell on pore width and not from a rapid increase in guard cell turgor pressure, as was widely supposed.



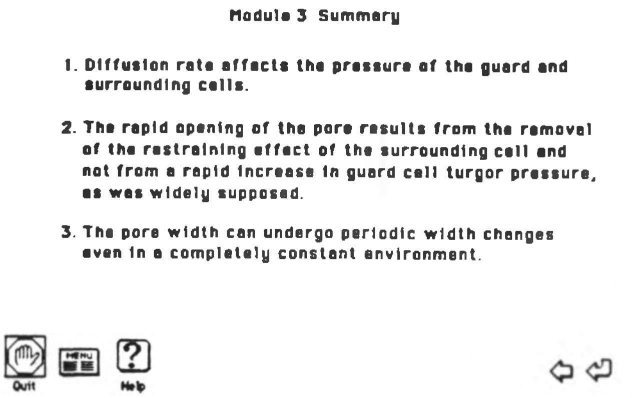
Notice that this conclusion could only have been discovered through a consideration of the behavior of the system. In other words, the vast literature on transport across isolated membranes could not have revealed this mechanism because the relationship of the guard cells, surrounding cells, and the rest of the plant must be considered simultaneously as a system. Previously we discussed the behavior of the system when subjected to a varying stimulus - the change in osmotic potential.



Click on the **Periodic Response** button to examine the periodic response which can occur under stress conditions.

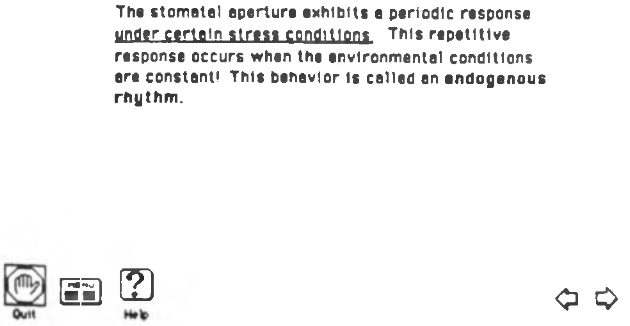
OR

Click on the continue arrow to skip this section.



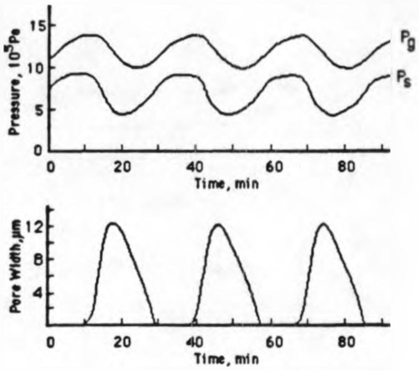
Module 3 Summary

1. **Diffusion rate affects the pressure of the guard and surrounding cells.**
2. **The rapid opening of the pore results from the removal of the restraining effect of the surrounding cell and not from a rapid increase in guard cell turgor pressure, as was widely supposed.**
3. **The pore width can undergo periodic width changes even in a completely constant environment.**

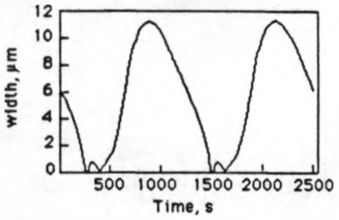


The stomatal aperture exhibits a periodic response under certain stress conditions. This repetitive response occurs when the environmental conditions are constant! This behavior is called an endogenous rhythm.

The figure at the right depicts such behavior. The guard cell and surrounding cell pressures oscillate with a period of roughly 20 minutes. Because the surrounding cell pressure reaches a minimum before the guard cell pressure does, the pore width oscillates, as shown in the lower figure.



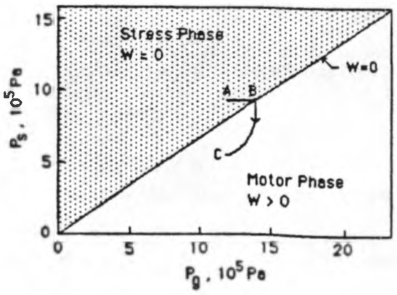
When we consider the carbon dioxide control system, an additional oscillation occurs after the pore closes and the internal supply of carbon dioxide becomes limiting. **Our calculations suggest that this behavior results in an improved water use efficiency!** In other words, the ratio of carbon assimilation to water loss increases.



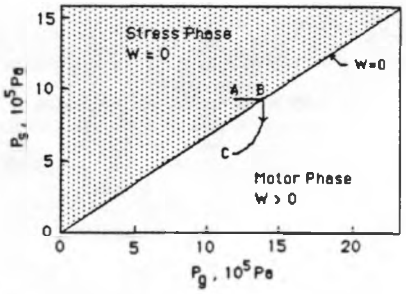
If this property of improved efficiency can be experimentally verified, it will present an interesting avenue for research into improved water use in agriculture. Perhaps irrigation requirements can be reduced through management practices or perhaps genetically adapted, more water efficient plants can be produced. [We are not aware of any reference in the literature to this beneficial characteristic of an endogenous rhythm.]

An Alternate Description of Stomatal Response

We have discussed the stomatal response as a function of time. Another interesting description results when the guard cell and surrounding cell pressures are the independent variables.



The figure at the left describes the transient response of pore opening considered earlier. Point A corresponds to the closed pore at time zero. The guard cell pressure increases to point B with no change in surrounding cell pressure.



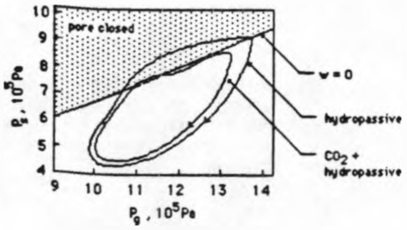
Next, the surrounding cell pressure decreases and the pore opens, i.e., the trajectory crosses the W=0 line and the pore opens. Both pressures decrease until a constant pore width at point C is reached. [Note. The pore width is proportional to the perpendicular distance from the W=0 line.]

Pore Width

Top view can be seen by clicking in this button.

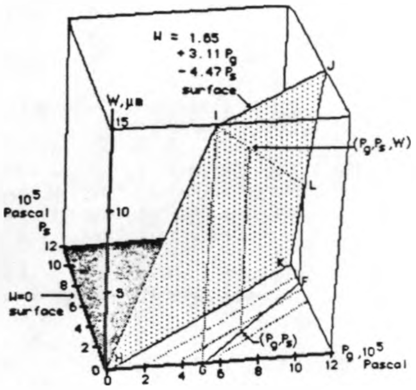
Periodic Response

The figure at the right shows the periodic response using the pressures as the independent variables. Note that the periodic response is a result of this trajectory crossing the W=0 line.

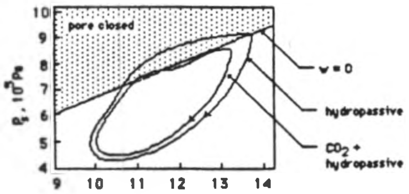


Limit cycle oscillation

Pore width cannot be negative, so the multilinear relationship is clipped to zero for those pressure combinations which would otherwise predict a negative pore width. Constant pore width lines are projected onto the pressure plane in the figure.



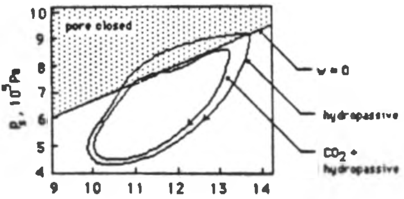
In other words, the clipping of the pore width relationship (i.e. movement into the pore closed region) produces the endogenous rhythm!



Limit cycle oscillation

Quit Help

The outer loop corresponds to the hydropassive control system. The inner loop corresponds to the combined hydropassive and carbon dioxide feedback loops. The effect of the carbon dioxide feedback loop is to keep the trajectory nearer the W=0 line; in fact, when the carbon dioxide becomes limiting, the pore opens slightly and then closes again.



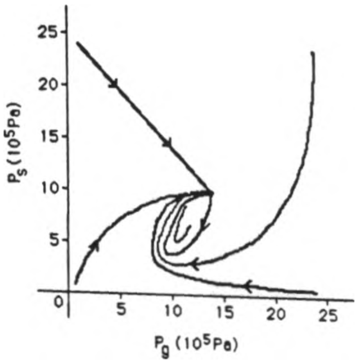
Limit cycle oscillation

Quit Help

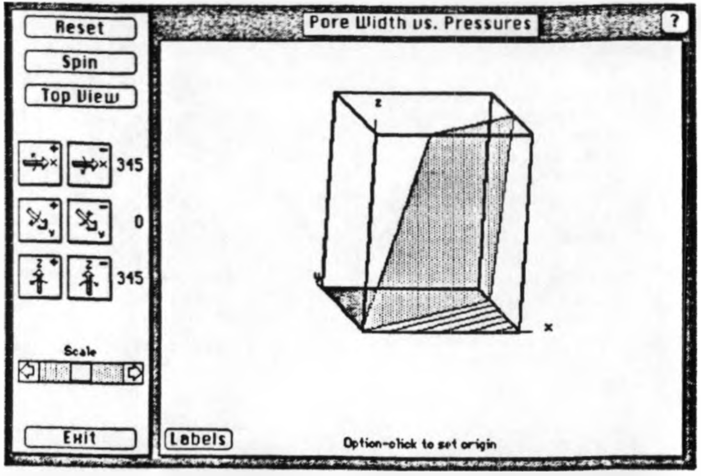
In the mathematical literature this periodic response is called a stable limit cycle. As the following illustrates, this periodic system response occurs regardless of the initial pressure combinations. Starting points inside and outside the stable limit cycle result in the same limit cycle being repetitively traced.

Quit Help

Starting points inside and outside the stable limit cycle result in the repetitive retracing of the same limit cycle.

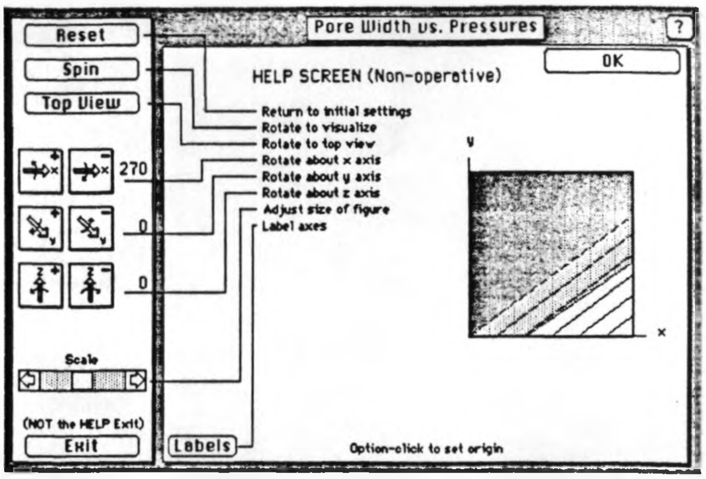


Quit Help



Pore Width vs. Pressures

Option-click to set origin



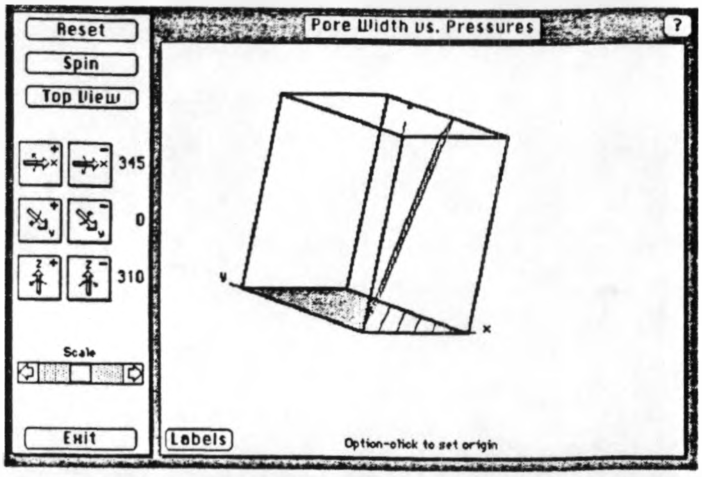
Pore Width vs. Pressures

HELP SCREEN (Non-operative)

- Return to initial settings
- Rotate to visualize
- Rotate to top view
- Rotate about x axis
- Rotate about y axis
- Rotate about z axis
- Adjust size of figure
- Label axes

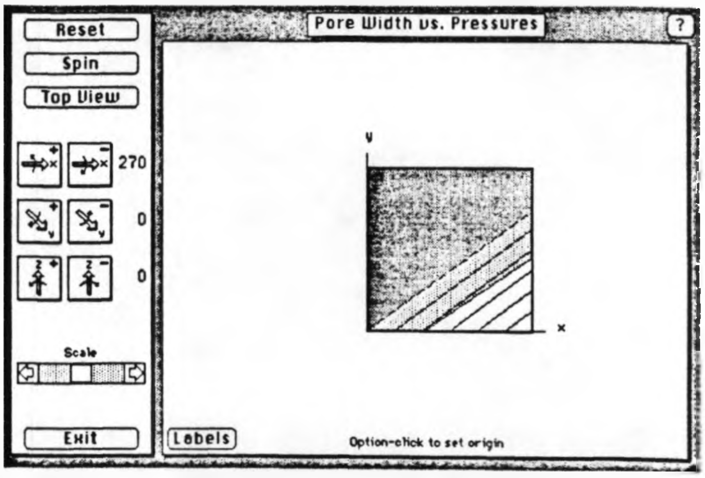
(NOT the HELP Exit)

Option-click to set origin



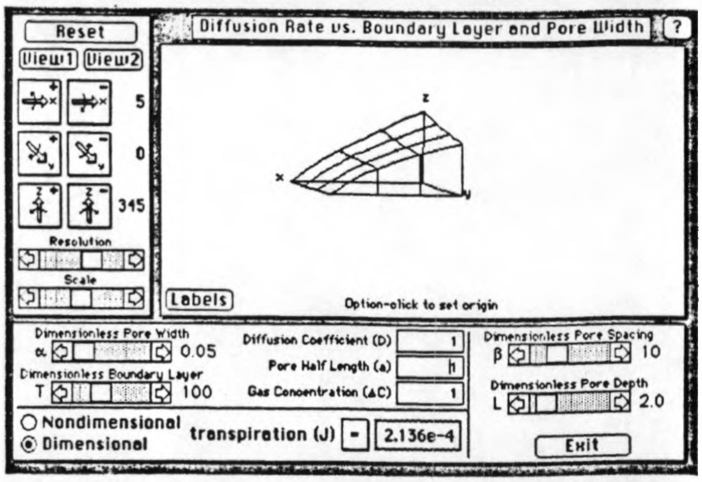
Pore Width vs. Pressures

Option-click to set origin



Pore Width vs. Pressures

Option-click to set origin



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

Diffusion Coefficient (D) 1

Pore Half Length (a) 1

Gas Concentration (ΔC) 1

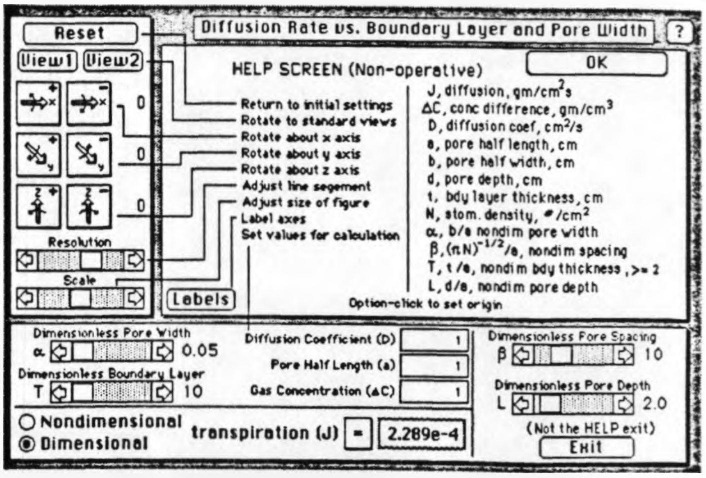
Dimensionless Pore Spacing β 10

Dimensionless Pore Depth L 2.0

○ Nondimensional

● Dimensional

transpiration (J) = 2.136e-4



Diffusion Rate vs. Boundary Layer and Pore Width

HELP SCREEN (Non-operative)

- Return to initial settings
- Rotate to standard views
- Rotate about x axis
- Rotate about y axis
- Rotate about z axis
- Adjust line segement
- Adjust size of figure
- Label axes
- Set values for calculation

J, diffusion, gm/cm^2s
ΔC, conc difference, gm/cm^3
D, diffusion coef, cm^2/s
a, pore half length, cm
b, pore half width, cm
d, pore depth, cm
t, bdy layer thickness, cm
N, stom. density, #/cm^2
α, b/a nondim pore width
β, $(\pi N)^{-1/2}/a$, nondim spacing
T, t/a, nondim bdy thickness, >= 2
L, d/a, nondim pore depth

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 10

Diffusion Coefficient (D) 1

Pore Half Length (a) 1

Gas Concentration (ΔC) 1

Dimensionless Pore Spacing β 10

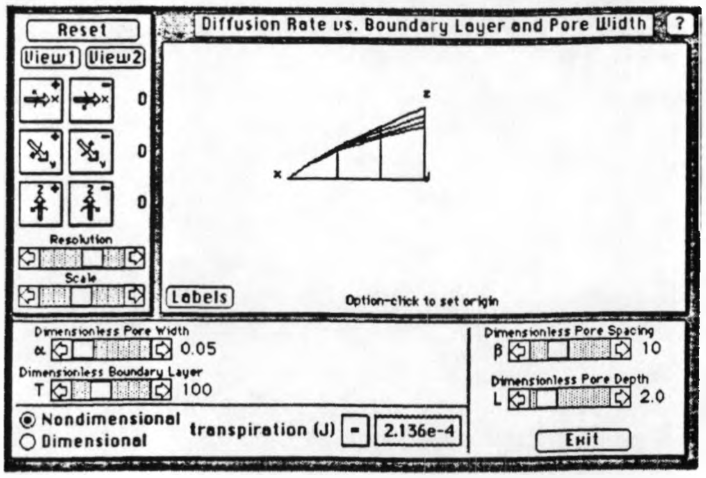
Dimensionless Pore Depth L 2.0

○ Nondimensional

● Dimensional

transpiration (J) = 2.289e-4

(Not the HELP exit)



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

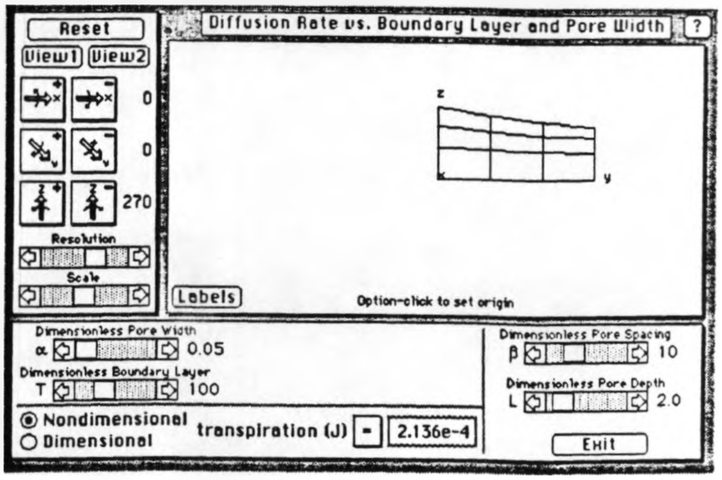
Dimensionless Pore Spacing β 10

Dimensionless Pore Depth L 2.0

● Nondimensional

○ Dimensional

transpiration (J) = 2.136e-4



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

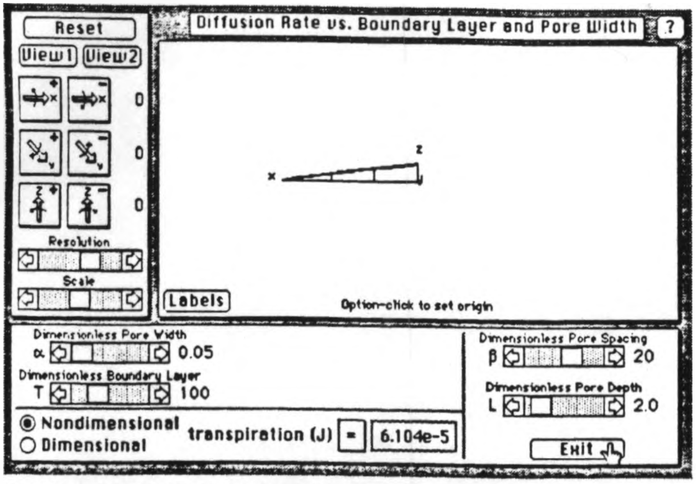
Dimensionless Pore Spacing β 10

Dimensionless Pore Depth L 2.0

● Nondimensional

○ Dimensional

transpiration (J) = 2.136e-4



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

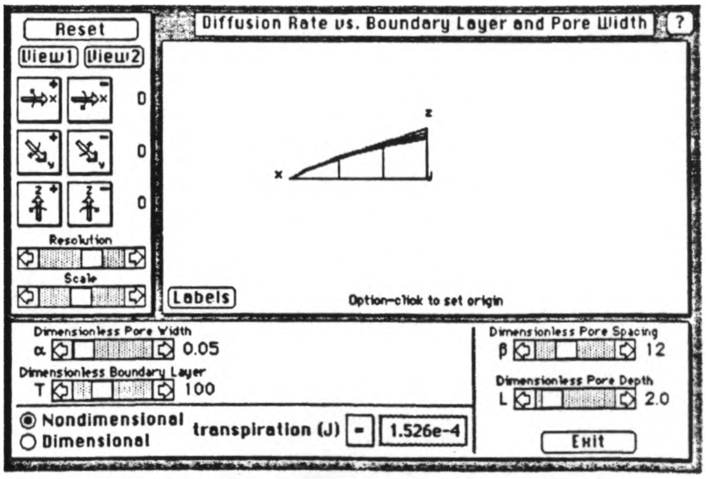
Dimensionless Pore Spacing β 20

Dimensionless Pore Depth L 2.0

● Nondimensional
○ Dimensional

transpiration (J) = 6.104e-5

Exit



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

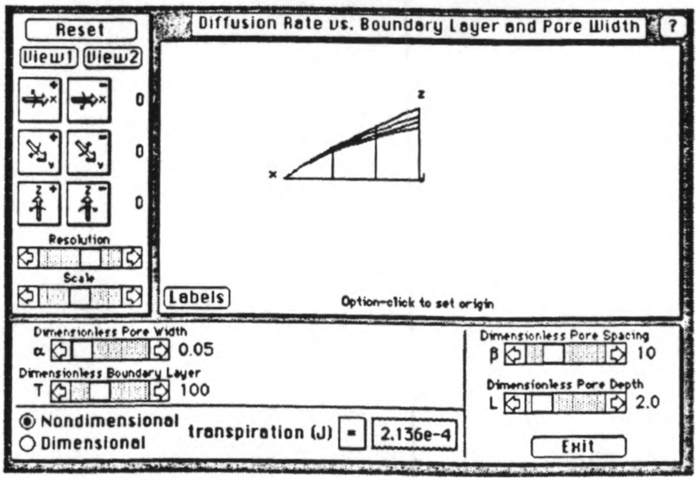
Dimensionless Pore Spacing β 12

Dimensionless Pore Depth L 2.0

● Nondimensional
○ Dimensional

transpiration (J) = 1.526e-4

Exit



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

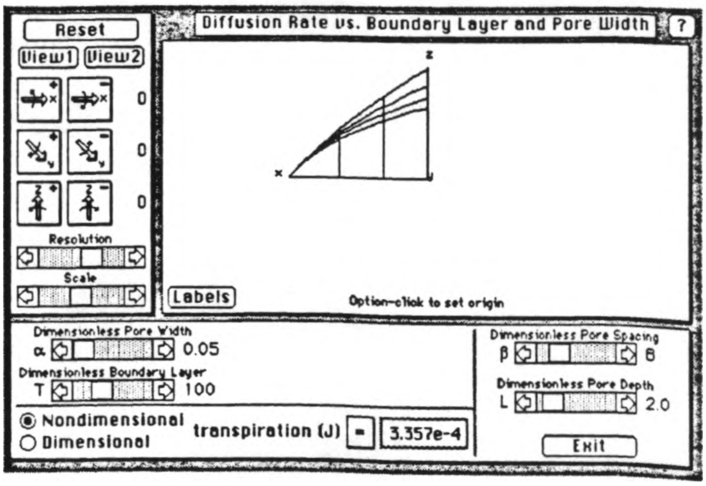
Dimensionless Pore Spacing β 10

Dimensionless Pore Depth L 2.0

● Nondimensional
○ Dimensional

transpiration (J) = 2.136e-4

Exit



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

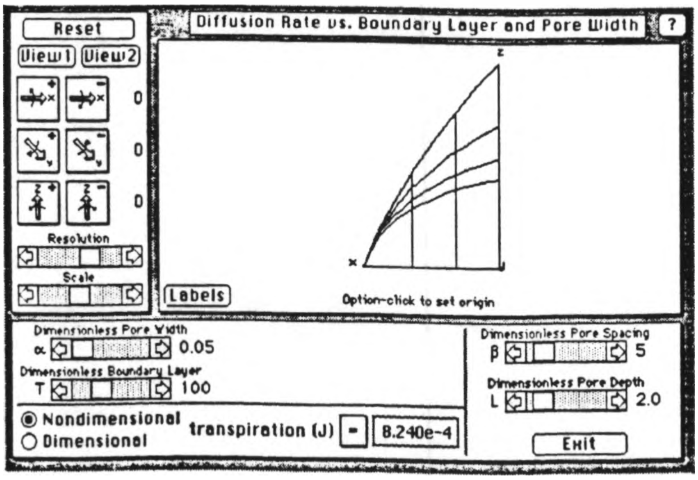
Dimensionless Pore Spacing β 8

Dimensionless Pore Depth L 2.0

● Nondimensional
○ Dimensional

transpiration (J) = 3.357e-4

Exit



Diffusion Rate vs. Boundary Layer and Pore Width

Option-click to set origin

Dimensionless Pore Width α 0.05

Dimensionless Boundary Layer T 100

Dimensionless Pore Spacing β 5

Dimensionless Pore Depth L 2.0

● Nondimensional
○ Dimensional

transpiration (J) = 8.240e-4

Exit