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Transpiration and the Stomata of Leaves

Water loss through leaf pores is controlled by pore size, which varies with environment and chemical sprays.

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Fully 71 percent of the precipitation received by the United States disappears through evapotranspiration from nonirrigated pastures, meadows, cultivated fields, forests, and noneconomic stands of plants. Further, about five times as much water is expended in irrigation as in industry (*1*). Part of the 1 million billion gallons (4 million billion liters) which escape each year through evapotranspiration escapes directly from the soil, but much —perhaps most—is transpired through leaf stomata or pores no larger than 35 by 15 microns. In other terms, evapotranspiration consumed 28 to 40 inches (81 to 102 cm) of the 76 to 80 inches of rain that fell on one North Carolina hardwood forest (*2*). We shall examine both the stomata themselves and their effect upon the diffusion or transpiration of water.

The stomata of a grass, maize, and of a broad-leafed plant, tobacco, are illustrated in Fig. 1. The upper and lower epidermes of maize and many other grasses are much alike and are perforated by stomata in about equal densities. In maize this density is approximately 10,000 stomata per square centimeter. During the day the guard cells at each side of the pore in a well-watered leaf separate as the swollen regions at each end enlarge. This movement opens a pore 1 to 6 microns wide and 25 microns long and exposes the moist leaf interior to the drier atmosphere outside.

Broad leaves of trees have practically no stomata in their upper epidermes. In the upper epidermes of many herbaceous broad-leafed plants, however, pores are quite densely distributed. Thus tobacco has about 4000 per square centimeter of upper and 8000 per square centimeter of lower epidermis. During the day the walls of the guard cells that border the pore become crescent shaped. This movement opens an elliptical hole 1 to 10 microns wide and 20 microns long, and thereby permits the transpiration of water.

"Previous work on the factors concerned in controlling transpiration has suffered from excessive concentration on the physical aspects of the process" (*3*). Since 1950 the outflow of papers concerning biological controllers, stomata, indicates that others share Gregory's opinion. Thus from 1945 to 1949, only 11 references to "stomata" were indexed in the *Bibliography of Agriculture*, but about 70 were indexed in each of the following 5-year periods. In 1964, alone, 35 were indexed.

In addition to the generally increased concern with water, two specific phenomena have heightened interest in stomata. First, progress in micrometeorology has refined the analysis of evapotranspiration sufficiently to require consideration of the influence of vegetation. Thus in 1951 Penman and Schofield (*4*) calculated from stomatal geometry a stomatal resistance to be added to the atmospheric resistance and provided a reasonable explanation for the roughly one-fifth deficiency of evapotranspiration compared to evaporation from a water surface. In 1963 Monteith (*5*) proposed that the resistance of the assembly of stomata in a field could be calculated by dividing evapotranspiration into the vapor-pressure deficit at the effective crop surface. The effective crop surface is the height where extrapolation of the wind profile above the crop gives a wind speed of zero. This resistance attributed to stomata and calculated from micrometeorological observations followed a diurnal course that corresponded to botanical ideas concerning stomata. Further, the resistance had the magnitude generally ascribed to that of stomata. Thus meteorologists have been concerned with stomata in their analysis of evapotranspiration from a field.

Another reason for recent interest is the discovery that stomata can be partially closed by a spray of about 10^{-4} molar solutions of several chemicals (*6, 7*). This opens the prospect of a test of the role of stomata in fully turgid, well-illuminated leaves. It also opens the prospect of practical control of evapotranspiration.

In the present discussion we shall treat first the mechanism of stomatal opening and closing and then the influence of stomatal aperture upon the diffusion of gas, particularly the water vapor that escapes the moist leaf interior.

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Turgor and Stomatal Opening

Stomatal opening is caused by turgor changes, and the difference in turgor between guard cells and their neighbors determines the aperture of the pore. Heath (*8*) elegantly demonstrated that making guard cells more or less flaccid than their neighbors caused them to close or open. If he punctured a sausage-shaped guard cell and thus made it flaccid, its side toward the pore became straight, and that half of the pore was closed. On the other hand, if a cell adjacent to the guard cell was punctured and the guard cell hence made more turgid than its neighbor, the guard cell became more curved, and that half of the pore was opened wider. Thus stomata open when their turgor increases relative to that of their neighbors, and they close when their turgor becomes relatively less. How these changes in turgor arise in nature is less clear.

Experiments have established that in many species stomatal width is affected by light, temperature, and carbon dioxide. In the following paragraphs these observations are combined with results from biochemical experiments in the search for a mechanism that creates the stomata-opening differences in turgor.

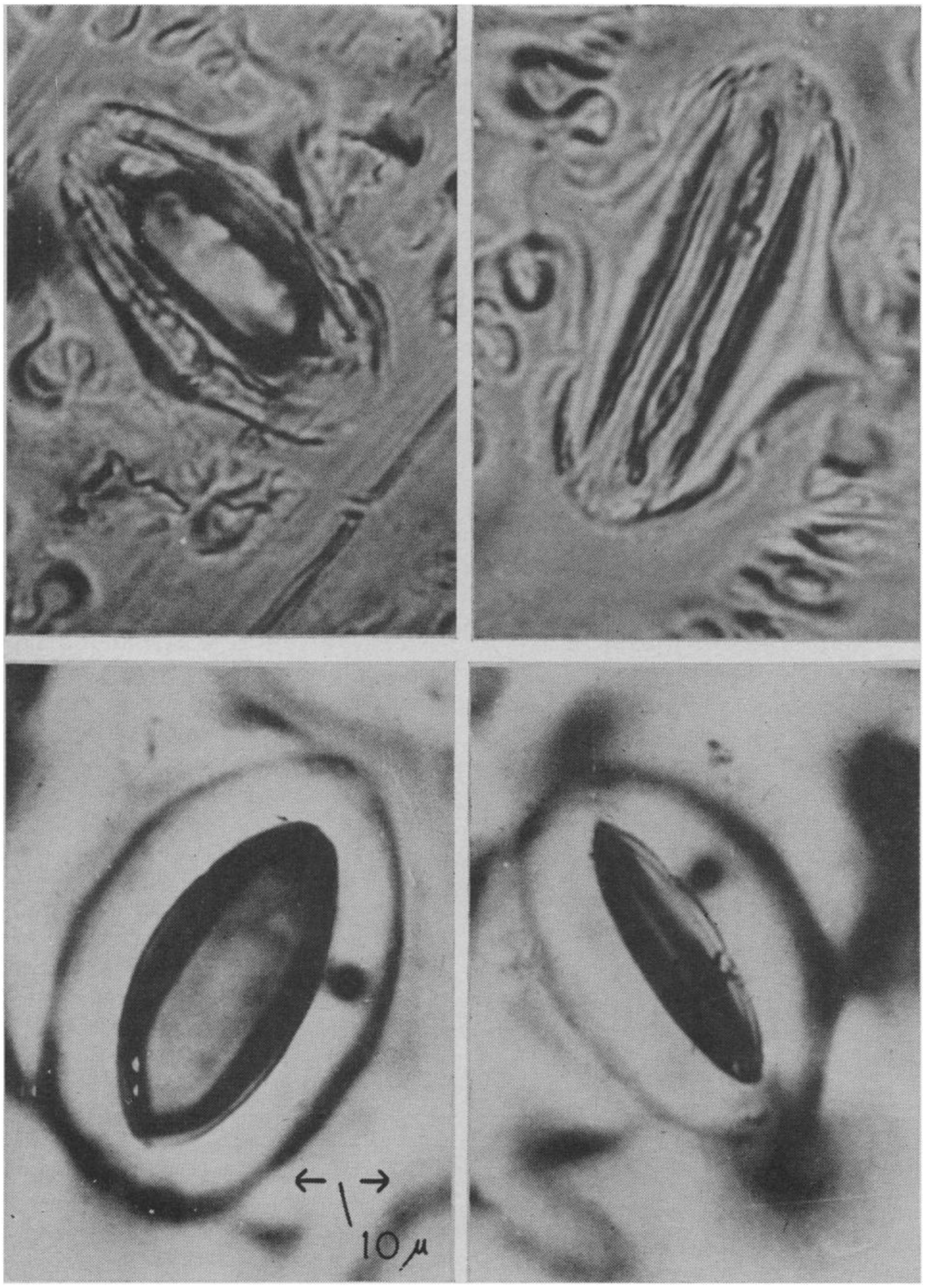

Fig. 1. Photographs from silicone rubber replicas of maize (top) and tobacco leaves (bottom). The scale applies to the actual stomata. The average length of tobacco stomata is 20 μ, and the one in the photograph is unusually long.

Environment and Opening

The presence of chloroplasts in guard cells is the most striking difference between guard cells and other epidermal cells. Past experiments have indicated that stomatal opening follows illumination of these chloroplasts (*9*). Recently, the spectrum for maintaining opening of stomata in isolated epidermis was found the same as the absorption spectrum of a dilute chloroplast suspension (*10*). Thus photosynthesis of the guard cell chloroplasts must be responsible for at least maintaining opening.

Higher temperatures have sometimes been accompanied by stomatal closure in the light, as in "midday closure," but this was probably caused by the drying of the warm leaf. With leaves actually floated on water, however, stomata widened as they warmed (*11*). When tobacco leaf disks were floated on water for 4.5 hours, their stomatal widths were 2.3 μ at 10°C and 7.7 μ at 30°C, and then quickly changed to a new aperture dictated by a new temperature to which they were transferred (*12*). Further, when intact well-watered maize leaves were warmed from 14° to 40°C, their stomata widened, diffusion resistance decreased, and photosynthesis and transpiration increased (*13*).

In the light, high concentrations of CO_2 cause stomata to close, and low concentrations cause them to open (*14*). Heath (*15*) has said that "the light response of the stomata may be entirely due to the removal of CO_2 by photosynthesis. . . ." Some results, however, suggest that opening is caused by essential products of photosynthesis rather than the depletion of CO_2 near the guard cells (*16*). This latter hypothesis requires that less of some essential product is produced as CO_2 concentration becomes very high, when photosynthesis increases and stomata close.

The effect of CO_2 concentration on the synthesis of glycolic acid in light behaves in such a fashion: stomatal opening and glycolic acid synthesis are similarly inhibited by a given concentration of CO_2 (*17*). Also, stomatal closing induced by 1.8 percent CO_2 could be largely reversed by floating the leaf on 0.001*M* glycolate, but not by a number of other substances.

The synthesis and oxidation of glycolic acid probably are important in stomatal opening because the glycolate-glyoxylate cycle (*18*) oxidizes the reduced form of nicotinamide-adenine dinucleotide phosphate and thus allows synthesis of adenosine triphosphate by noncyclic photophosphorylation (*19*) to proceed rapidly (*20*). The energy of adenosine triphosphate may thus be available to operate the guard-cell "pump."

Biochemical Inhibitors

Scattered observations of stomatal closure after chemical treatment have been made in the past. These seem never to have been followed up, perhaps because they were made casually, because they were not reproducible, or —more likely—because the chemicals were extremely toxic (*21*).

One of the first observations that stomata could be closed without causing a generalized toxicity to the plant appears to have been that of M. M. Ventura (*22*). He placed excised leaves of *Stizolobium* in dilute solutions of sodium arsenite, 2,4-dinitrophenol, or Janus green and found that each decreased stomatal opening and transpiration. Also, 8-hydroxyquinoline sulfate closed stomata (*23*).

At this Station the finding that α-hydroxysulfonates, which are effective competitive inhibitors of glycolate oxidase (*24*), prevent stomatal opening in light led to the development of a standard leaf-disk assay for investigating stomatal movement (*6*). Leaf disks of tobacco have the advantage of large stomata that open and close relatively uniformly. In the assay, leaf disks with closed stomata are floated on water, or the solution to be tested, for 90 minutes at 30°C in the light. Stomatal apertures are then measured from silicone rubber impressions (*6*) of the lower epidermis (Fig. 1).

The standard leaf-disk assay permits rapid determination of whether a given compound effectively prevents stomatal opening. With three different inhibitors, we found a good correlation between closure in the disk assay and the closure observed several hours after tobacco leaves were sprayed with solutions of these reagents (*7*).

Although the disk assay has proven useful, it has limitations: it does not reveal the length of time closure will last after a single spraying, or whether the compound will be toxic or translocated. Nor does the assay indicate whether CO_2 uptake will be inhibited in cells other than the guard cells.

The inhibitors of stomatal opening can be classified into large groups. All known inhibitors but one interfere only with opening in the light. The exception, sodium azide, in addition to inhibiting opening also interferes with closing in the dark if the concentration is high enough (*12*).

Alternatively, the inhibitors may be grouped into those which affect metabolic reactions that increase the turgor of the guard cells (the "pump"), or those which alter the permeability of the cell membrane (the "check valve"). The α-hydroxysulfonates, which were mentioned earlier, and sodium azide at low concentrations are believed to interfere with the pump (*20*). The compounds discussed in the following paragraphs are presumed to affect mainly the check valve.

Previously some compounds effective in the standard tobacco disk assay have been listed, together with the concentrations of each which bring about 50-percent closure (*20*). Phenylmercuric acetate is outstanding in that it produces this result at $5 \times 10^{-5}M$. The closure induced by spraying phenylmercuric acetate on tobacco leaves lasted 2 weeks and did not greatly affect growth (*7*). Phenylmercuric acetate probably reacts with sulfhydryl groups in membranes of the guard cells and accordingly alters their permeability (*20*).

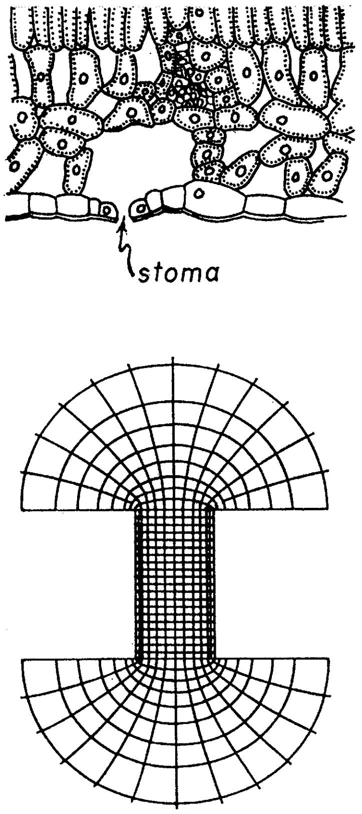

Fig. 2. Cross section of a tobacco stoma (top) and the diffusion and decrease in concentration of water through a stoma as idealized by Brown and Escombe (bottom). The tobacco stoma is reprinted with permission of Macmillan Company, from H. E. Hayward, *Structure of Economic Plants* (*48*), fig. 28, p. 76. Copyright 1938 by Macmillan Company.

Several compounds, including herbicides, inhibited transpiration when sprayed on bean plants at concentrations from 1.0 to $1.7 \times 10^{-3}M$. Some more effective substances were: "Atrazine" (2-chloro-4-ethylamino-6-isopropylamino-*s*-triazine), isopropyl-*N*-phenylcarbamate, "Karsil" [*N*-(3,4-dichlorophenyl)-2-methylpentanamide], 3,4-dichloropropionanilide, 5-bromo-3-isopropyl-6-methyluracil, and phenylmercuric acetate (*25*). Presumably these compounds closed stomata, although stomata were not directly observed. Karsil and Atrazine may operate by reacting with membranes (*26*).

Phenylhydrazones of carbonyl cyanide at $10^{-4}M$ inhibit stomatal opening in the disk assay (*20*). Since these compounds are uncouplers of both oxidative and photosynthetic phosphorylation (*27*) and inhibit formation of adenosine triphosphate, they presumably close stomata by interfering with both the pump and the check valve.

Alkenylsuccinic acids and their derivatives, $CH_3\text{-}(CH_2)_n\text{-}CH{=}CH\text{-}CH_2\text{-}CH(COOH)\text{-}CH_2COOH$, close stomata at low concentrations in the disk assay. The most effective compounds are the monoethyl and monoglyceryl esters of decenylsuccinic acid ($n = 6$) (*28*). The same structures that close stomata increase the permeability of bean roots to water. They also eliminate the temperature-dependence of water transport across root cell membranes, as would be expected if the hydrocarbon chains of the lipid layers were separated, thus making the membranes more porous (*29*). It is therefore likely that the alkenylsuccinic acids prevent stomatal opening by causing the plasma membrane of the guard cell to increase in permeability with subsequent loss of turgor in these cells.

History of Resistance Studies

Analysis of the regulation of gaseous diffusion by stomata, like the problem of guard-cell movement, has been vexed. But a valid analysis has been published for over half a century; recently it seems well authenticated, although the notorious Perimeter Law can still be found in current publications.

In 1900 Brown and Escombe (*30*) visualized the diffusion of water vapor through a stoma as diagrammed in the lower part of Fig. 2. Three regions of resistance to diffusion were visualized: First, the concentration of lines of flow inside and near the stoma, then the resistance through the stomal tube, and finally, outside and near the stoma, a resistance equal to the one inside.

The resistance in the tube itself was simply set at the length l divided by the cross-sectional area πr^2 and K, the coefficient of diffusion of water in air. Since the theoretical diffusion of a wet disk of radius r is $4Kr$ times the difference in water concentration between disk and air, they set the resistance of each region at the tube ends equal to $1/4Kr$. Thus the resistance of n stomata per square centimeter was

$$\frac{1}{nK}\left(\frac{l}{\pi r^2}+\frac{2}{4r}\right)\text{ sec cm}^{-1} \qquad (1)$$

They then calculated the water that should diffuse from a *Helianthus* leaf whose temperature was the same as that of the air. The relative humidity of the air was 25 percent. Since this predicted transpiration was six times the fastest rate that they had ever observed, they concluded that "the relatively large amounts of water which pass out of the leaf may be fully accounted for by *diffusion only*." They were not concerned that their hypothesis predicted much more transpiration than they ever observed, which indicated that a goodly portion of the diffusion resistance had been overlooked.

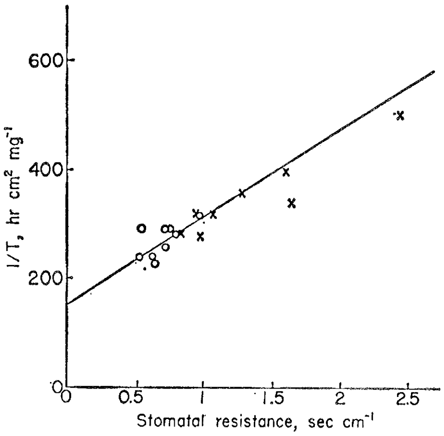

Fig. 3. Relation between reciprocal of transpiration (T) and stomatal resistance in unsprayed (O) tobacco leaves and tobacco leaves sprayed with phenylmercuric acetate (X).

In 1910 Renner (*31*) added to the resistance visualized by Brown and Escombe the resistance of the still atmosphere that is outside the outer hemisphere of Fig. 2. This was necessary on commonsense grounds, for without this addition the formula of Brown and Escombe shows no resistance and hence predicts infinitely rapid diffusion from an open evaporator. This simple concept of resistance of the atmosphere, in fact, removes the necessity for the complicated consideration of interference between adjacent stomata (*32*). Renner assumed that atmospheric resistance in calm air from a leaf as a whole is $1/4KR$ where R is the leaf radius, but his experiments showed that in practice is was nearer $1/4\pi KR$. Penman and Schofield (*4*) later encountered the same smallness of resistance when they analyzed Brown and Escombe's data and attributed it to the difficulty of obtaining the still air specified in the theory. Thus Renner stated that the resistance of a square centimeter of the leaf in still air is

$$\frac{R}{4K}+\frac{1}{nK}\left(\frac{l}{\pi r^2}+\frac{2}{4r}\right)\text{ sec cm}^{-1} \qquad (2)$$

In wind, $R/4K$ was assumed to become zero and $2/4r$ to become $1/4r$.

Renner increased the estimate of resistance considerably. Thus Brown and Escombe calculated the resistance of the system in Fig. 2 to be 0.31 sec cm^{-1} in a *Helianthus* leaf, and Renner would add $R/4K$ or 5 sec cm^{-1} for a 5-cm leaf. Renner's estimate would then be more consistent with the data; whereas Brown and Escombe predicted that transpiration would be fully six times greater than the fastest observed rate, the prediction from Renner's equation would be less than the maximum. Specifically, Brown and Escombe calculated 1730 g m^{-2} hr^{-1} and observed a maximum of only 276, compared to a theoretical 88 according to Renner. Compared to the 1730, the 88 is more plausible, for it is less than the maximum or extreme ever observed, while being nearer to it.

Much of Renner's work was a demonstration that an earlier opinion that stomata regulated transpiration only when closed or nearly closed was erroneous. He measured stomatal dimensions and transpiration in eight genera, predicted the transpiration from Eq. 2, and saw the prediction verified. Despite this clear and early demonstration of a logical theory, the matter of regulation of diffusion by stomata was soon clouded.

In 1926 Sayre (*33*) observed the diffusion of water through perforated films into still air. He considered only the same part of the resistance as Brown and Escombe did. So great was the neglected resistance of the still air that the diffusion did not increase as rapidly as the radius of the pores, and Sayre chose the perimeter of elongated pores as a less variable parameter than the radius.

This was the foundation of the Perimeter Law: "Diffusion rates through small openings vary as the perimeter, not the area. . . . Since diffusion of gases through stomates is proportional to the perimeter of the pore, diffusion rates through a partially open stomate are almost as great as when the stomate is fully open" (*34*). Ample evidence exists, however, that stomata affect transpiration in the logical manner that Renner demonstrated and hence throughout the range of stomatal width.

Thus the transpiration from a *Betula* leaf increased when the stomatal width increased from 4 to 8 μ (*35*), and transpiration through the large pores of a ventilated *Zebrina* leaf doubled when they widened from 5 to 15 μ (*32*).

Stomatal Resistance and Transpiration

The remarkable degree to which stomatal behavior explains variation in transpiration can be calculated by linear correlation. The reciprocal of transpiration T is related linearly to stomatal resistance:

$$\frac{1}{T}=\frac{\Omega}{\Delta x}+\left(\frac{l}{\pi r^2}+\frac{1}{2r}\right)\Big/\underline{nK\Delta x} \qquad (3)$$

In this case, Ω is the resistance of the atmosphere and Δx is the difference between the concentration of water in the free air and in the air deep within the substomatal cavity. In an experiment, nine pairs of excised tobacco leaves were observed on nine different days. During the one-hour exposure, transpiration was measured, and at the end of the exposure the dimensions of replicas of the stomata were measured. Their widths varied from 1 to 10 μ. One-fourth the product of the length times the width of the elliptical stomatal openings was substituted for r^2 in Eq. 3. Ninety percent of the variability of the reciprocal of the transpiration from these 18 leaves was accounted for by stomatal resistance, Fig. 3 (*7*).

Similar outcomes have been obtained with intact maize plants (*36*). Accordingly, there seems little reason to doubt that stomata throughout the range of stomatal width affect the rapidity of transpiration from a single leaf or an isolated plant.

Even though the relative change in transpiration per 1 μ change in stomatal width will never be zero, it will, not always be the same. An obvious factor controlling the relative change can be seen in expression (2); the radius r itself. The greater the radius, the smaller the change in either stomatal or total resistance per 1 μ change. Thus stomatal resistance (Eq. 1) is decreased 44 percent when the width of an elliptical pore increases from 1 to 2 μ, but only 13 percent when it increases from 5 to 6 μ. These estimates were calculated for a stomatal depth l of 10 μ and a length of the elliptical opening of 25 μ, but the percentages would change little if the depth or the length of the opening were twice as large.

The shape of the walls, however, affects the percentages considerably. For example, the curvilinearity of the walls of barley stomata had to be taken into account before the conductivity or reciprocal resistance of these pores could be explained (*37*). The monocotyledonous stomata have nearly rectangular openings, and instead of πr^2 and $2r$ in Eq. 1 length times width and the square root of length times width were substituted. The mouths of these stomata were found to be about 0.6 throat width plus 4 μ. If the curve of the sides can be represented by a sine curve, then the conductivity of the stomata increases as the upper, more curvilinear graph of Fig. 4. The lower curve pertains to stomata with straight sides. Clearly the relative change in transpiration is more rapid per 1 μ change in width at narrow widths if "width" pertains to the throat of a pore with curved sides rather than to a straight tube.

The relative change in transpiration will be somewhat less than the above changes in stomatal resistance or conductance, because the total resistance to transpiration (Eq. 2) includes an independent term, the resistance of the air above the leaf.

Renner simply set the resistance of a square centimeter of the leaf as $R/4K$ (Eq. 2) in still air and as zero in the wind. Actually, of course, this resistance does not disappear but varies inversely roughly with the square root of the wind velocity. In any event, Ω in Eq. 3 and the intercept of the regression line with the ordinate in Fig. 3 are less when the leaf is well ventilated. Then the relative change in $1/T$ and in transpiration are greater for a given change in stomatal width and resistance. In like manner, the change in transpiration with changed ventilation is greater when the stomata are wide.

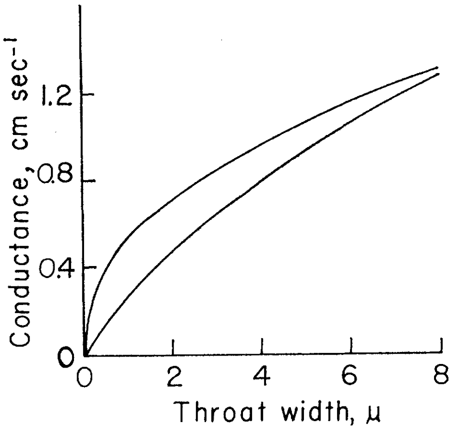

Fig. 4. Relation between stomatal conductance in barley, assuming curved walls (upper curve) and straight walls (lower curve).

Observations of the transpiration of *Zebrina* illustrate clearly the interrelation in the control of transpiration of stomatal width and ventilation. In the case of a well-ventilated leaf, the curve for transpiration plotted against size of stomatal aperture rises sharply from zero aperture and continues to increase rapidly to 20 μ. When the leaf is in still air, however, the graph rises very slowly from 5 to 20 μ, (Fig. 5). Thus when the stomata widen from 5 to 20 μ, the transpiration from a leaf in still air increases only two-thirds but that from a wind-swept leaf nearly triples (*32*). The resistance also decreases with the narrowness of the leaf. If one would demonstrate the control of transpiration by stomata, he should observe a narrow leaf in a brisk breeze rather than a broad leaf in a calm chamber.

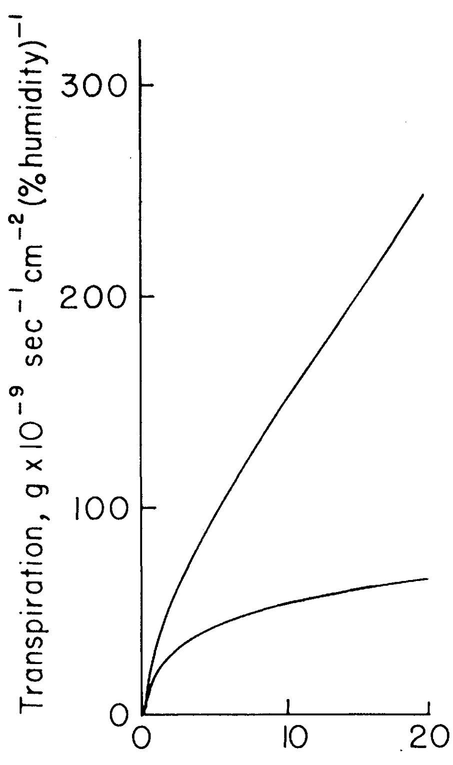

Fig. 5. Relation between transpiration and stomatal width in *Zebrina* in wind (upper curve) and still air (lower curve) (*32*).

A third source of resistance to the transpiration of soil water exists, in addition to that of stomata and atmosphere, and may be considerable although it has not been entered in the mathematical expressions. This is the resistance of the soil and plant that causes the air in the stomatal cavities to be unsaturated. When maize grew in soil with 13 percent water, transpiration was considerably less than when it grew in soil with 24 percent water, although stomatal aperture was the same (*36*). Thus the greatest resistance of the plant to the transpiration of water undoubtedly lies in the stomata, but we must be aware that other resistance surely exists and may sometimes be considerable.

Leaf Temperatures

Since stomatal apertures, and hence resistance, always influence the transpiration of an isolated leaf or plant, and sometimes greatly, they will also influence leaf temperature. The latent heat of transpiration is generally a large account in the daytime energy budget of the leaf. Hence anything, such as stomatal resistance, that changes the transpiration will require a change in the difference between the temperature of the leaf and its surroundings. This will alter the radiation and convection accounts and bring the budget again into balance.

The energy budget of a leaf has been written in terms that permit estimation of the difference θ between air and leaf temperature (*38*). The atmospheric exchange coefficients involved in evaporation and convection are assumed to be equal, exchange is assumed to be uniform over the leaf surface, and the air deep within the substomatal cavities is assumed to be at leaf temperature and saturated with water.

The energy budget is written as the sum of radiation, convection, and evaporation. Each of these three accounts is in turn written as the sum of exchange if the leaf were at air temperature, plus a correction for the difference θ. The budget can be solved for θ and examples calculated. The examples in Table 1 pertain to the realistic example of a sunlit leaf that would gain 0.01 cal cm^{-2} sec^{-1} by radiation on its two faces and that is in air whose temperature is 30°C and humidity 50 percent. The atmospheric resistances Ω of a 5- and of a 15-cm leaf were calculated (*39*) to be 1.7 and 2.3 sec cm^{-1} in 5-cm-sec^{-1} ventilation (0.1 miles per hour) and 0.25 and 0.35 in a 223-cm-sec^{-1} breeze (5 miles per hour). The stomata of the example are 10 μ deep, have elliptical openings 25 μ long, are of variable width, and have a density of 10,000 per square centimeter. Then stomatal resistance (Eq. 1), with an elliptical area substituted for πr^2, is ∞, 2.8, and 0.77 sec cm^{-1}, respectively, when stomata are 0, 1, and 5 μ wide. The effect upon the difference between leaf and air temperature can be seen in Table 1. Thus when stomata open from 0 to 1 μ, much energy that was formerly radiated and convected and that required a large θ is lost through transpiration, and the leaf becomes cooler. Alternatively, if the stomata are 5 μ wide, the leaf becomes warmer when the stomata narrow to 1 μ. The temperature difference between leaf and air is affected more by width when ventilation is slight or the leaf is large. Like transpiration, the leaf temperature is changed when stomata widen from 1 to 5 μ as well as from 0 to 1 μ.

Observations agree with the above calculations. When a cotton leaf was sprayed with $10^{-5}M$ phenylmercuric acetate, its stomatal resistance approximately quadrupled, and its transpiration decreased one quarter in slowly moving air. When transpiration diminished one quarter, the leaf warmed 1° to 5°C (*40*). For the preceding tabulation, we calculated that when stomata narrow from 5 to 1 μ in 5-cm-sec^{-1} ventilation, stomatal resistance would approximately quadruple, total resistance would increase by three quarters, and the leaf would warm 3° to 5°C, a satisfactory agreement with the observations (*40*).

Table 1. Effect of ventilation on temperature difference for various stomatal widths.

Wind speed (cm sec^{-1})	Temperature difference (C°)		
	Width 0 μ	Width 1 μ	Width 5 μ
	5-cm leaf		
5	14.5	5.0	1.4
223	3.6	1.1	−1.8
	15-cm leaf		
5	16.7	6.1	2.9
223	4.8	1.4	—1.8

The warming of the leaf when stomata close moderates the decrease in transpiration that would otherwise occur. That is, the difference Δx in water concentration between substomatal cavities and the atmosphere increases as stomatal resistance increases and hence diminishes the subsequent decrease in transpiration. The operation of this phenomenon can be seen in the example of the 5-cm leaf when stomata narrow from 5 to 1 μ. In only 5-cm-sec^{-1} ventilation stomatal resistance nearly quadruples and total resistance nearly doubles, but transpiration decreases by only one fifth because the leaf becomes warmer and the water concentration difference increases by about half. In the 223-cm-sec^{-1} breeze, however, quadrupled stomatal resistance triples total resistance and decreases transpiration by one-half. The warming of the leaf that follows increasing stomatal resistance will decrease the slope of Eq. 3. Thus both the cooling of the leaf and the minimizing of Ω are reasons why the decrease of transpiration through stomatal movement is better demonstrated in well-ventilated leaves than in becalmed ones.

Photosynthesis

Photosynthesis must be mentioned because the ingredient, carbon dioxide, diffuses through the same openings that pass water vapor. Since stomatal resistance is in the series of resistances that control the diffusion of carbon dioxide, as it is in the series for water, stomatal movement will always change photosynthesis as it does transpiration, unless countervailing changes occur. The relative effect is, of course, determined by the other resistances; the larger they are, the smaller the change in CO_2 uptake.

In the case of transpiration it was realistic to ignore the resistance between soil and substomatal cavities and consider only the moderation by Ω. In photosynthesis, a third resistance must be added, for CO_2 also diffuses through the water surrounding the chloroplasts. If we consider transpiration proportional to atmospheric plus stomatal resistance and photosynthesis proportional to the sum of the same two resistances plus an additional mesophyll resistance, the narrowing of stomata should decrease transpiration relatively more than photosynthesis does. This result has been observed in tobacco (*7*), maize (*36*), and cotton (*40*) when stomata were sprayed and narrowed with phenylmercuric acetate solution.

At least three phenomena could modify this. Improved hydration with decreased transpiration could actually increase photosynthesis as occurred in maize growing in soil that contained only 10 percent water (*36*). On the other hand, decreased transpiration could so warm the leaf that transpiration would change no more than photosynthesis. If the device employed to close stomata decreases the photosynthetic ability of the mesophyll, photosynthesis might even decrease more than transpiration. Nevertheless, in tobacco, maize, and cotton, transpiration decreased more than photosynthesis when stomata were narrowed.

Isolated Plants Outdoors

The foregoing evidence that narrower stomata in isolated leaves or plants in the laboratory decrease transpiration is interesting. But the important matter is the outcome outdoors. Given the normal stomatal apertures of a well-watered plant outdoors, is the total resistance of plant and atmosphere, or even of a stand of plants and the atmosphere, materially increased when the stomata narrow? We shall first consider isolated plants and then stands of plants.

The decrease in transpiration of an isolated plant outdoors should be similar to that of one in the laboratory. Stomatal widths outdoors are generally not greater than those indoors. Brisk ventilation is common outdoors. A spray that closes stomata—the device that we shall consider—can be applied evenly to all leaf surfaces of an isolated plant. This is necessary because the chemicals that we have studied are not translocated; lack of translocation has the advantage of affecting fewer cells beyond the guard cells but requires that guard cells be struck by the spray.

Sunflowers were grown outdoors in soil contained in concrete bins. Although interfering rain was excluded by a plastic roof and evaporation from the soil was prevented by a film, the sides of the enclosure were open and the plants were essentially "outdoors." When the plants were 24 days old, their stomata were closed by a spray of $90 \times 10^{-6}M$ phenylmercuric acetate. A porometer that forced air through the leaves indicated that stomata were narrower where sprayed. For 37 days afterwards soil water was extracted 14 percent more slowly from beneath the sprayed than from beneath the unsprayed plants, although the leaf area was only 2 to 5 percent less (*41*).

Jack pines, about 30 centimeters tall, were grown under a similar roof in cans that contained about 11 kilograms of soil. In mid-July some of the plants were sprayed with 0.3×10^{-3} and some with $10^{-3}M$ phenylmercuric acetate. During five subsequent drying periods in the course of the ensuing 38 days, the sprayed plants lost a significant 17 and 21 percent less water than the unsprayed ones. In another experiment, $10^{-3}M$ inhibitor decreased transpiration 20 percent during the same period. The weight of new growth, part of which was produced after spraying, was not changed significantly (*42*).

Ten jack pines, about 140 centimeters tall, were grown in the open, but the roots of each were in a lysimeter 50 centimeters in diameter and 75 centimeters deep. During the growing season about a third of the rainfall and irrigation leached through. Five trees were sprayed four times with $10^{-3}M$ phenylmercuric acetate. Evapotranspiration was decreased 2 percent and leachate increased 16 percent by the treatment. We presume but do not know that spraying closed stomata. The sprayed plants appeared lighter green than the unsprayed by midsummer, but this could not be detected in the following spring (*42*).

These three experiments indicate that transpiration from isolated and well-watered plants outdoors can be decreased by spraying the leaves with an inhibitor that closes stomata. (Needless to say, transpiration cannot be decreased if drought has already stopped it.)

Spraying To Conserve Water

Many practical difficulties in the spraying of vegetation for water conservation can be conjured up. The cost of spraying and, even more important, the long-term effects upon plants and animals are specters that come to mind.

The fundamental hydrologic problem, however, is whether spraying a chemical that narrows stomata upon a stand of plants—a crop or a forest—will substantially decrease transpiration and hence conserve soil water and increase stream flow. Unlike the isolated plant, the stand is far different from the leaf in the laboratory. Stomatal width is not different, but ventilation of leaves within the stand may be slow, and spraying all leaf surfaces seems impractical. Further, since several acres of leaves grow on each acre of land, there may be so many stomata per acre that stomatal resistance may be negligible compared to other resistances, as long as stomata are open the least crack. We shall consider the magnitude of stomatal resistance in a stand, then the effect of spraying only some of the stomata, and finally, experiments in actual water conservation in the field.

The micrometeorologist's new concern with stomatal resistance was mentioned earlier. In 1951, Penman and Schofield (*4*) regarded the stand as an "extremely large flat leaf . . . for as transpiration rates are mainly determined by incoming energy supply, the important quantity is the projected surface on a horizontal plane; the evaporation from a wet blotting paper is not increased by putting another wet piece underneath it." Their Ω for reasonable wind speeds would be 1.2 to 0.8 sec cm^{-1}. They assumed 20,000 stomata per square centimeter and stomatal resistance of 0.3 sec cm^{-1} during the daytime. (If the stomata had straight sides 10 μ deep and elliptical openings 20 μ long, their width would be 7.2 μ.) This estimated transpiration reasonably well. We calculate that narrowing the stomata from 7.2 to 3.6 μ would increase stomatal plus atmospheric resistance 15 to 20 percent in 200- to 400-cm-sec^{-1} wind. Presumably, therefore, evapotranspiration from a closed stand could be diminished about one sixth by narrowing stomata to half their prior width.

Estimation of stomatal resistance from meteorological parameters, as described in the introduction, provides values of midday stomatal resistance of about 0.5 sec cm^{-1} in long grass and 1.0 in well-watered beans, surprisingly close to that for a single epidermis. During a drought, the stomatal resistance in beans increased to 3.0. The Ω in the beans was about 1.0 (*5*). Once again, a reason is provided for expecting a considerable decrease in transpiration from a change in stomatal width.

The remaining concern is the impracticality of spraying all stomata in a stand. Not all stomata are important conductors, however. Those in the lower part of the stand are shaded in a moist and relatively calm environment. Further, the stomata of lower leaves are likely to be closed (*43*). Thus within the stand closed stomata and an environment with little potential for evaporation sharply decrease the number of layers participating in transpiration and affecting stomatal resistance in the stand. If this were not so, the meteorological estimates for the crop would not have nearly equalled the stomatal resistance of a single leaf as mentioned in the preceding paragraph.

Only the problem of spraying the undersides of upper leaves remains. Thus halving the widths of only the 4000 stomata per square centimeter in the upper side of a tobacco leaf will theoretically decrease by 14 percent transpiration through these and the 8000 per square centimeter in the lower surface. If, however, only 400 perforated the upper surface, the same halving would decrease transpiration only 3 percent (*44*). In an extreme example, spraying only the stomata-free upper surface of tree leaves will have no effect. We can conclude that spraying and narrowing the stomata in the upper surfaces of upper leaves may substantially reduce transpiration from a stand of plants that have a considerable portion of their stomatal conductance in those upper surfaces.

In fact, this has already been tested. When the stomata-free upper surfaces of the broad-leaved trees on a watershed were sprayed, stream flow was unaffected (*45*). When, however, a stand of barley was sprayed from above with a similar chemical, the stomata were narrowed and evapotranspiration was decreased 13 to 30 percent (*46*).

Some plants, of course, naturally have great stomatal resistance. Thus Renner (*31*) long ago calculated that the 30-μ deep tubes above the sunken stomata of *Agave* decreased transpiration one-third in this desert plant. And drought-resistant Coastal Bermuda

Grass has much narrower stomata than drought-susceptible Dallis-Grass (*16, 47*). The preceding paragraphs of theory and observation awaken hope that these savings might be produced when willed.

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The Schools Lectures at the Royal Institution

The Institution provides a "repertory theater" of scientific experiments to be shown to young people.

Lawrence Bragg

The Royal Institution has a long and famous history. It was founded in 1799 by Count Rumford (Benjamin Thompson) at a time when there was a growing interest in Natural Philosophy and when "Literary and Philosophical Societies" were being formed in many centers. The founder, however, designed for it a structure more ambitious than that of other institutions, and although he failed to realize all his aims, his originality and foresight gave the Institution a unique character which it has retained. Not only was it to be a place where the intelligentsia would meet each other, hear discourses about science, and consult a library of scientific books and periodicals, it was also to include what we would now call a research center and a technical college. It was to have professors who, as well as informing the members of advances in science, were to do original work in the Institution's laboratories. It was to have classes for mechanics, because Rumford was convinced that they would do their work more efficiently and with greater interest if they knew something of the scientific basis of craftsmanship. One of Rumford's great interests was the application of scientific principles to objects of everyday use—grates, stoves, chimneys, ventilation systems, cooking utensils, clothing—and many of the things we take for granted nowadays—for example, the kitchen range, the pressure cooker, the coffee percolator, and the double-walled saucepan—are Rumford's inventions. His plans for training mechanics failed; he was before his time and was defeated by apathy and misunderstanding. On the other hand, his plan for combining the popular exposition of science with original research was gloriously successful, and these two functions have set the pattern for the Royal Institution for more than 150 years. For the first three-quarters of the 19th century, in the great days of Humphry Davy, Faraday, and their successors, it was the "center" for the physical sciences in Great Britain.

I have given this brief account of the history of the Royal Institution in order to sketch in the background for my description of the Institution's Schools Lectures. The Royal Institution is a private body, supported by its members' subscriptions, its endowments, and donations given by industrial and other bodies in recognition of its educational work. Being a private body, it is free to make experiments on its own initiative and to start new ventures.

The Christmas Lectures

One such venture, which has since become famous, was started in the year 1826. It was a course of six lectures "adapted for a Juvenile Auditory," given in the fortnight after Christmas. The Christmas Lectures have been held every year since then, except when interrupted by the two world wars. They are planned for young people between 12 and 17, though in the "Juvenile Auditory" all

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