The Stomatal Apparatus: The Path of the Gas Supply in Plants

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In that remote age when the ancestors of our present day plants left the aquatic environment and became adapted to land conditions, they had to undergo severe changes. Whereas they had been accustomed to being surrounded by water, they had, under the new conditions, to resist the drying effects of the atmosphere. If they had developed a water-proof skin the difficulty would have been solved : but a water-proof skin is also a gas-proof skin ; and a plant, like an animal, needs to have gaseous oxygen to enable it to respire ; unlike an animal, it also needs gaseous carbon dioxide (which it takes in and makes into starch, cellulose, sugars, proteins and most of those substances which constitute the plant body). Thus a gas-proof skin would mean that the plant would be unable to get the gas necessary for its food or the gas necessary for its energy.

The plants were virtually faced with two kinds of death—on the one hand by drying up, on the other hand by starving to death through lack of gas. The situation was saved by a compromise, and the result was the delicate complicated structure which is visible in a leaf under the microscope. This resultant development of leaf structure was by no means sudden, and it has taken many, many years for all the diverse leaf forms to evolve.

Chloroplasts.

The appearance of a section cut through a leaf from one side to another examined under a microscope is shown in the diagram (Fig. I). Both the upper and lower surfaces have a water-proof skin (the cuticle), which is on the outside of the protecting layer of cells (the epidermis). This water-proof skin enables the inside of a leaf to have a number of cells which are (save under exceptional circumstances) filled with water : not only are they filled with water, but they have porous walls which are always damp. These cells have certain inclusions inside them, all of which have functions. Among the contents of the cell are the green bodies (chloroplasts) which appear circular. These small green bodies are able to take the gas carbon dioxide and, in the presence of sunlight, turn it into sugars which the plant can use and build into other substances. When we consider that man and all other animals depend either directly or indirectly on plants for their food, and that all plants depend on the presence of these tiny chemical laboratories—the chloroplasts—we realise their importance as the ultimate source of the world's food supply.

Stomates.

Given cells full of water, the green chloroplasts, light, and the gas carbon dioxide, the plants will build their food. The gas must enter the leaf through the water-proof skin; so that the compromise that allowed plants to develop on land was the system of openings through the epidermis. These openings are known as stomates. Naturally they play a very important part in the story of the land plant's general physiological processes. If we regard the leaf as a complicated food factory, we can regard these openings—the stomates—as the importing department. They import the carbon dioxide for the food; they import the oxygen which the plant uses in respiration as a source of energy; but they do more than that. Sometimes the leaf itself produces either of these gases in excess; then the stomates become eliminators of waste products. Again, sometimes the economy of the factory is upset by external

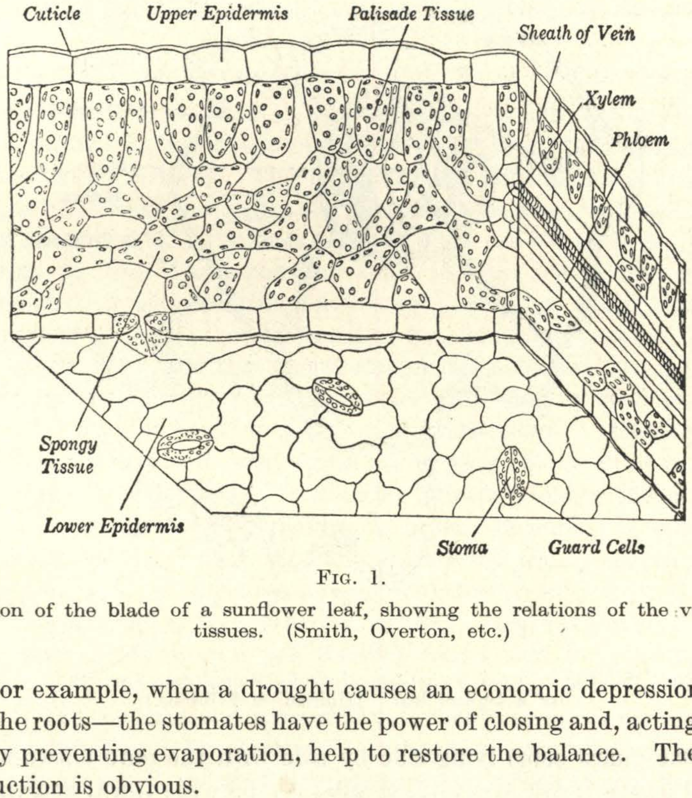

FIG. 1.

Portion of the blade of a sunflower leaf, showing the relations of the various tissues. (Smith, Overton, etc.)

conditions—for example, when a drought causes an economic depression in the water supply from the roots—the stomates have the power of closing and, acting as conservers of moisture by preventing evaporation, help to restore the balance. Their importance in crop production is obvious.

Stomates, then, are the openings through the skin communicating between the inside of the leaf and the outside air. They have the power of opening and shutting. The leaf has no pumping system, so that gases which move in and out through the stomates can do so only by diffusion.

GAS DIFFUSION.

A gas is composed of a very large number of tiny particles (molecules) which are constantly moving about, and which tend to distribute themselves evenly through the available space. Thus, as the cells in the leaf use the gas, more moves in through the stomates, because there are a greater number of particles in a given volume outside than inside. On the other hand, if the gas is being produced inside the leaf, there are relatively a greater number of particles inside, so they move out, to the outside air. The open stomate allows the gas to move freely in or out ; but if the stomates are closed, this movement or diffusion of gas is prevented.

The Behaviour of the Stomate.

The stomate is a very tiny organ ; on that account its ability to open and close is all the more interesting. As the diagram (Fig. II) shows, it consists of two sausage-

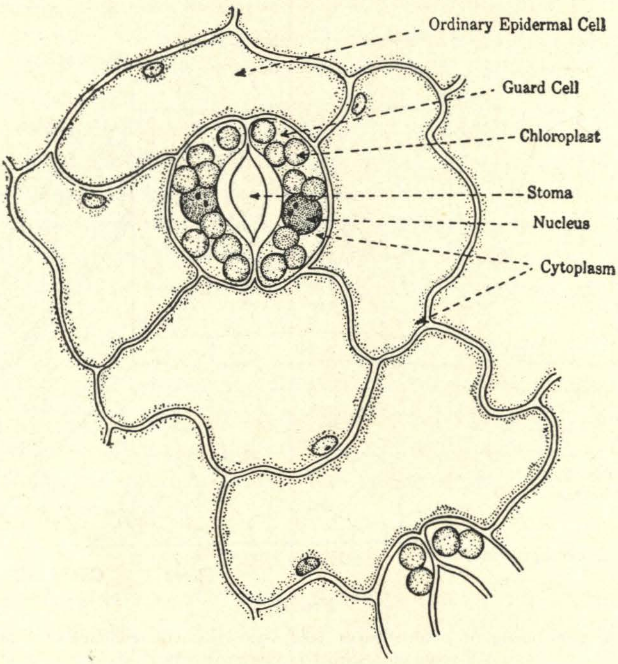

Fig. 2.
A view showing in detail a small portion of the epidermis from the surface of a typical leaf. (Holman & Robbins.)

shaped cells (the guard cells) lying side by side with the pore between them. The cells are joined at the ends ; the walls against the pore are thick, and the distal walls are thin. If these two cells are full of water, the walls distant from the pore stretch : but the thick walls are inextensible, so they are pulled apart and the stomate opens. When the cells lose water they collapse together and the pore closes. The same effect can be obtained by laying two pieces of rubber tubing side by side, joining them together at each end and pumping air simultaneously into both pieces. This causes the two pieces to separate and leave a space between them.

The Size of Stomata.

The number of stomata occurring on the leaf surface varies between about 25 per square millimetre and some 300 per square millimetre in different plants. Though they are usually very numerous, they are too small to be seen with the naked eye; and in some plants the actual pore measures only about $\frac{1}{100}$ millimetre in length, by about $\frac{3}{1,000}$ millimetre in width. Thus the sum total of openings in the surface of the leaf is very small indeed—usually something of the order of 1 to 2%. When it is considered that the concentration of carbon dioxide in the atmosphere is only 0·03%, and that it takes quite a large volume of carbon dioxide to make one gramme even of simple sugar, it seems remarkable that the gas diffuses sufficiently rapidly through this 1 to 2% of opening. Some experiments by Brown and Escomb on the diffusion of gases through multiperforate septa help us to understand this phenomenon.

The Relation between Area and Rate of Diffusion.

It has long been known that Dalton's formula, which shows that the rate of diffusion of gas, say from a liquid, is proportional to the area of the evaporating surface, does not hold for small surfaces. This is because the diffusion away from the edges is more rapid than that from the centre. This is obvious when we consider a crowd of people coming out of a gate. The ones near the posts can get away first, because they can spread out to the sides, but the ones in the centre are jostled in the general confusion; so with diffusing molecules. Stephan found that the rate of diffusion from small surfaces is proportional to the diameters, and not to the areas.

Brown and Escomb found that this diameter law holds for multiperforate septa. It follows logically that diffusion will take place more rapidly through several small openings than through one large opening equal in diameter to the total of the small apertures. Brown and Escomb went further, and were able to show that the spacing of the perforations is important. Considering crowds coming through gates, it is sufficiently obvious that a crowd will move more rapidly through several small separated gates than through one large one. If the gates are too widely spaced it may not be possible to fit in enough per unit area to cope with the crowd; if, on the other hand, they are too closely placed, they will "interfere" with each other, and the same jostling will occur. Thus Brown and Escomb found that for multiperforate septa the optimum spacing of the holes was a separation by ten times the diameter of the perforation. If the perforations are properly spaced, then, though the membrane must offer some resistance, the amount of obstruction is surprisingly small, and the rate of diffusive flow may be almost as great as if the septum were absent altogether.

The epidermal apparatus with stomates open possesses the physical properties of a multiperforate septum; and, with favourable conditions of moisture supply and wide open stomates, the rate of diffusion may be almost as great as if no cuticle were present. If, due to a deficiency of moisture supply, the conditions become unfavourable, the stomates can, by closing, almost completely block the communication between the internal and external atmospheres. The advantage of such a system to the plant is quite obvious.

Stomatal Behaviour.

The behaviour of stomates varies in different plants and with different conditions. After extensive work, Loftfield found that he could divide the plants he examined into three groups according to their stomatal behaviour. Nearly all the plants examined since fit into one or other of these three groups. The three types of behaviour distinguishable are as follows :

(1) *The Cereals.*—The stomates of this group are open in the day. Night opening does not occur under ordinary conditions, favourable or unfavourable. Day opening is dependent in duration and degree upon favourable conditions.

(2) The second group Loftfield called the *thin-leaved mesophytes.* The stomates are open all day and closed all night under favourable conditions. As conditions become less favourable, a day closure appears. With less favourable conditions this day closing becomes more extended, until it may occupy the whole day. Night opening appears when mid-day closure occurs, and increases in degree and extent with it. Finally under extreme conditions the stomates are closed all day and open all night, the degree of opening depending on the moisture supply.

(3) The third group of plants, which Loftfield called the *fleshy-leaved plants,* tends to have the stomates open day and night under optimum conditions, especially of moisture supply. When the moisture decreases, the stomates tend to become more and more sensitive to light. They then open with daylight and close with night. If the water content becomes critical the effect of sunlight can be modified, or even nullified, by the evaporation, this producing day closure and night opening.

It is obvious from these differences in stomatal behaviour that the explanation is not a simple universal one. It is also sufficiently clear that stomatal movement does not depend on any one factor like light, or moisture supply, but that it is at times profoundly affected by changes in both these factors.

THE FUNCTION OF STOMATAL MOVEMENTS.

In the light of our knowledge of the behaviour of stomates, let us look at the possible functions for this behaviour. Early observers assumed that the stomates—since they were the passage for diffusion of water vapour, and since they opened and shut at different times—were delicate controllers of transpiration (the loss of water vapour from the leaves).

Critical experimental work soon showed this assumption was unjustified. Attacks were made by Lloyd, who is at present visiting Sydney and lecturing under the auspices of the University Extension Board, and by Knight. Knight showed that transpiration is controlled to a large extent by the water content of the leaf ; a high water content tends to high transpiration rate ; low water content tends to low transpiration rate. At the same time stomatal aperture is not reduced by slight water deficit in the leaf. The plant, indeed, has an internal regulating mechanism which, as Maximov says, is far quicker to act and far surpasses in its effect the regulative action of the closing stomates. This, of course, does not mean that the closure of stomates is not important from the point of view of moisture conservation. It is important, and helps the plant considerably, *but the stomates must be considered as conservers of moisture during hard times, and certainly not, under ordinary conditions, as controllers of the transpiration rate.* Loftfield considers that the effects of external factors are not masked by the closure of stomates until the stomates are more than half closed.

(To be continued.)