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**Topic- Stomatal regulation of transpiration**

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# Stomatal regulation of transpiration

The loss of water in the vapour form from the exposed parts of a plant is called transpiration. The loss of water due to transpiration is quite high —2 litres per day in Sunflower, 36—45 litres in Apple and up to 1 tonne per day in Elm tree. Rather 98-99% of the water absorbed by a plant is lost in transpiration. Hardly 0.2% is used in photosynthesis while the remaining is retained in the plant during growth.

**Types of Transpiration:**

Most of the transpiration occurs through foliar surface or surface of the leaves. It is known as foliar transpiration. Foliar transpiration accounts for over 90% of the total transpiration.

Young stems, flowers, fruits, etc. also transpire a lot. Mature stems transpire very little. Transpiration from stems is called cauline transpiration. Depending upon the plant surface transpiration is of the following four types— stomatal, cuticular, lenticular and bark.

**i. Stomatal Transpiration:**

It is the most important type of transpiration. Stomatal transpiration constitutes about 50-97% of the total transpiration. It occurs through the stomata. The stomata are found mostly on the leaves. A few of them occur on the young stems, flowers and fruits.

The stomata expose the wet interior of the plant to the atmosphere. The internal air, therefore, becomes saturated with water vapours. The outside air is seldom saturated with water except just after rains.

Water vapours, therefore, pass outwardly through stomata by diffusion. More water evaporates from the internal cells to replace the outgoing water vapours (Fig. 11.32). The stomatal transpiration continues till the stomata are kept open.

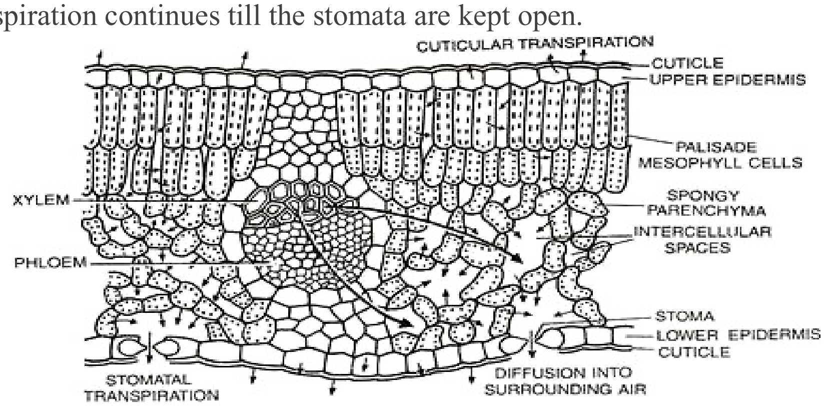


Fig. 11.32. V.S. leaf showing stomatal and cuticular transpiration.

**ii. Cuticular Transpiration:**

It occurs through the cuticle or epidermal cells of the leaves (Fig. 11.34) and other exposed parts of the plant. In common land plants cuticular transpiration is only 3-10% of the total transpiration. In herbaceous shade loving plants where the cuticle is very thin, the cuticular transpiration may be up to 50% of the total. Cuticular transpiration continues throughout day and night.

**iii. Lenticular or Lenticellate Transpiration:**

It is found only in the woody branches of the trees where lenticels occur. The lenticular transpiration is only 0.1% of the total transpiration. It, however, continues day and night because lenticels have no mechanism of closure. The lenticels connect the atmospheric air with the cortical tissue of the stem through the intercellular spaces present amongst the complementary cells.

**iv. Bark Transpiration:**

This type of transpiration occurs through corky covering of the stems. Bark transpiration is very little but its measured rate is often more than lenticular transpiration due to larger area. Like cuticular and lenticular types of transpiration, bark transpiration occurs continuously during day and night.

**Stomatal Apparatus**

Stomata (= stomates) are tiny pore complexes found in the epidermis of leaves and other soft aerial parts. The size is 10- 14 µm (range 7-38 pm) in length and 3-12 µm in breadth. The number of stomata per $cm^2$ of leaf surface varies from 1000- 60,000 or 10-600/$mm^2$.
In mesophytic plants, stomata occur both on the upper (adaxial) and lower (abaxial) surfaces. Their number is roughly equal on the two surfaces in grasses and other monocot leaves. In dicot leaves, the number of stomata on the upper surface is usually smaller, even absent in several cases.

Stomata are meant for the gaseous exchange but are also the main source of transpiration. Each stomate or stoma is surrounded by two small but specialized green epidermal cells called guard cells. Because of their small size, they are rapidly influenced by turgor changes. The guard cells are connected with the adjacent epidermal cells through plasmodesmata.

They contain a few small chloroplasts with peripheral reticulum characteristic of chloroplasts showing $C_4$ photosynthesis. The guard cells also possess small vacuoles and micro bodies.

They store starch with the exception of a few. The walls are differentially thickened and elastic. They have folds for expansion. Micro fibrils of these walls are oriented specifically to help in opening and closing of stomata.

In most of the plants the guard cells are kidney shaped in outline (Fig. 11.35 A-B). They are joined at their ends. The concavo-convex curvature of two guard cells is variable and causes stomatal pore to open and close. The walls of these guard cells are thickened on inner side. They have one or two pairs of wall extensions or ledges to prevent entry of water drops into stomata.

The walls are thinner and more elastic on the outer side. When the stomata are to open, these guard cells swell up on the outer side by the development of a high turgor pressure. The inner concave sides also bend out slightly so as to create a pore in between two guard cells. During closure movement, reverse changes occur.

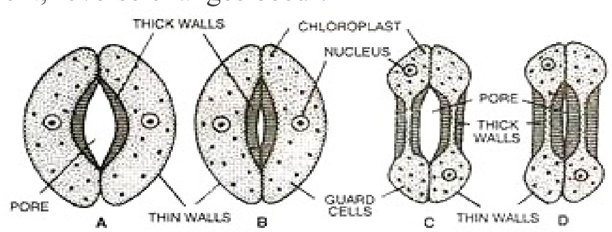


Fig. 11.35. Opened and closed stomata.
A. Dicotyledonous. B, Monocotyledonous.

In cereals, members of cyperaceae and some plams the guard cells are dumb-bell shaped in outline (Fig. 11.35 C-D). Their expanded ends are thin-walled while middle portions are highly thick-walled. In such cases opening and closing of the stomatal pore is caused by expansion and contraction of thin-walled ends of the guard cells.

**Mechanism of Stomatal Movement:**

Stomata function as turgor-operated valves because their opening and closing movement is governed by turgor changes of the guard cells. Whenever, the guard cells swell up due to increased turgor, a pore is created between them. With the loss of turgor the stomatal pores are closed.

Stomata generally open during the day and close during the night with a few exceptions. The important factors which govern the stomatal opening are light, high pH or reduced $CO_2$ and availability of water. The opposite factors govern stomatal closure, viz., darkness, low pH or high $CO_2$ and dehydration.

**There are three main theories about the mechanism of stomatal movements:**

**i. Hypothesis of Guard Cell Photosynthesis:**

Guard cells contain chloroplasts. During day the chloroplasts perform photosynthesis and produce sugar. Sugar increases osmotic concentration of guard cells. It causes absorption of water from nearby epidermal cells. The turgid guard cells bend outwardly and create a pore in between. However, photosynthetic activity of guard cell chloroplasts seems to be negligible.

**ii. Classical Starch Hydrolysis Theory:**

The main features of the theory were spelled out by Sayre (1923). It was modified by Steward (1964). The guard cells contain starch. At low carbon dioxide concentration (in the morning achieved through photosynthesis by mesophyll and guard cells), pH of guard cells rises.

It stimulates enzyme phosphorylase. Phosphorylase converts starch into glucose 1-phosphate. The latter is changed to glucose 6-phosphate which undergoes hydrolysis to produce glucose and phosphoric acid.

$$\text{Starch} + nH_3PO_4 \xrightarrow{\text{Phosphorylase}} n\ \text{Glucose 1-phosphate}$$

$$\text{Glucose 1-phosphate} \underset{}{\overset{\text{Phosphoglucomutase}}{\rightleftharpoons}} \text{Glucose 6-phosphate}$$

$$\text{Glucose 6-phosphate} + \text{water} \xrightarrow{\text{Phosphatase}} \text{Glucose} + H_3PO_4$$

Glucose increases osmotic concentration of guard cells. On account of it, the guard cells absorb water from neighbouring cells, swell up and create a pore in between them.
Evening closure of stomata is brought about by increased carbon dioxide content (due to stoppage of photosynthesis) of leaf. It decreases pH of guard cells and brings about phosphorylation of glucose. In the presence of phosphorylase, glucose 1-phosphate is changed into starch.

$$\text{Glucose} + \text{ATP} \xrightarrow{\text{Hexokinase}} \text{Glucose 6-phosphate} + \text{ADP}$$

$$\text{Glucose 6-phosphate} \overset{\text{Phosphoglucomutase}}{\rightleftharpoons} \text{Glucose 1-phosphate}$$

$$\text{Glucose 1-phosphate} \xrightarrow{\text{Phosphatase}} \text{Starch} + H_3PO_4$$

As a result, osmotic concentration of guard cells falls. They lose water to adjacent epidermal cells. With the loss of turgidity, the guard cells shrink and close the pore in between them.

**Objections:**

(i) Glucose is not found in guard cells at the time of stomatal opening,

(ii) Starch ↔ Sugar changes are chemically slow while opening and closing of stomata are quite rapid,

(iii) Wide changes in pH of guard cells cannot be explained on the basis of carbon dioxide concentration,

(iv) Onion and some of its relatives do not possess starch or related polysaccharide that can be hydrolysed to the level of glucose,

(v) Blue light has been found to be more effective than other wavelengths for opening of stomata. The same cannot be explained by starch hydrolysis theory,

(vi) Hydrolysis of starch theory cannot account for high rise in osmotic pressure found in guard cells.

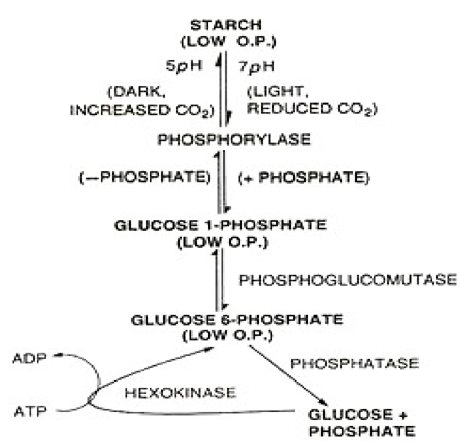


Fig. 11.36. Development of high and low osmotic pressures in guard cells through starch hydrolysis theory.

**iii. Malate or $K^+$ ion Pump Hypothesis (Modern Theory):**

The main features of the theory were put forward by Levitt (1974). According to this theory, pH of the guard cell can rise due to active $H^+$ uptake by guard cell chloroplasts or mitochondria, $CO_2$ assimilation by mesophyll and guard cells. A rise in pH causes hydrolysis of starch to form organic acids, especially phosphoenol pyruvate. Starch → Hexose Phosphate → Phosphoenol Pyruvate.

Phosphoenol pyruvate can also be formed by pyruvic acid of respiratory pathway. With the help of PEP carboxylase (PEP case), it combines with available $CO_2$ to produce oxalic acid which gets changed into malic acid.

Malic acid dissociates into $H^+$ and malate. $H^+$ ions pass out of the guard cells actively. In exchange, $K^+$ ions pass inwardly. Same $Cl^-$ ions may also enter guard cells along with $K^+$ ions. Guard cells maintain their electroneutrality by balancing $K^+$ with malate and $Cl^-$ (Fig. 11.37).

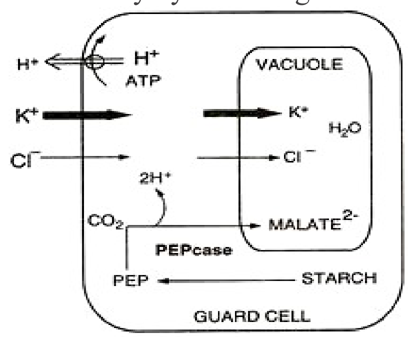


Fig. 11.37. Role of $K^+$, $Cl^-$ and malate in increasing osmotic concentration (decreasing water potential) of guard cells.

In the combined state they pass into the small vacuoles and increase the osmotic concentration of the guard cells. As a result guard cells absorb water from the nearby epidermal cells through endosmosis, swell up and create a pore in between them.

During stomatal closure, the $H^+$ ions diffuse out of the guard cell chloroplasts. It decreases pH of the guard cell cytoplasm. Any malate present in the cytoplasm combines with $H^+$ to form malic acid.

Excess of malic acid inhibits its own biosynthesis. High $CO_2$ concentration also has a similar effect. Un-dissociated malic acid promotes leakage of ions. As a result $K^+$ ions dissociate from malate and pass out of the guard cells.

Formation of abcisic acid (as during drought or midday) also promotes reversal of $H^+$ = ↔ $K^+$ pump and increases availability of $H^+$ inside the guard cell cytoplasm. Loss of $K^+$ ions decreases osmotic concentration of guard cells as compared to adjacent epidermal cells.

This causes exosmosis and hence turgidity of the guard cells decreases. It closes the pore between the guard cells. Simultaneously the organic acids are metabolised to produce starch.

**Factors Affecting Stomatal Movements:**

Stomatal movements are influenced by a number of environmental factors like light, temperature, humidity, water availability and $CO_2$ concentration. Internal or endogenous factors include growth hormones, organic acids, $K^+$, $Cl^-$ and $H^+$ ions.

**i. Light:**

In the majority of plants the stomata open in light and close in darkness. The light intensity required for stomatal opening is quite low (250 ft. candles in Tobacco). Even moon light is sufficient in some cases.

Both red and blue parts of light are effective though the latter is slightly more effective. However, in succulents or CAM plants (crassulacean acid metabolism), the stomata remain closed during daytime. They open only during dark, e.g., Agave, Opuntia, and Pineapple.

**ii. Temperature:**

$Q_{10}$ for stomatal opening is two. At 38°- 40°C, stomata can open in complete darkness, while at 0°C they remain closed even in continuous light. Normally high temperature above 30°C reduces stomatal opening in many species.

**iii. Atmospheric Humidity:**

In humid environment the stomata remain opened for longer periods while in dry environment they remain closed for longer periods.

**iv. Water Availability:**

Plants undergo water stress if availability of water is less than the rate of transpiration. Water stress (= water deficit = moisture deficit) brings about stomatal closure due to ABA and rise in DPD of epidermal cells.

**v. Mechanical Shock:**

It causes closure of stomata.

**vi. $CO_2$ Concentration:**

Low $CO_2$ concentration usually induces opening of stomata while high $CO_2$ concentration closes the same. In some plants mere breathing over the leaves causes stomatal closure.

However, guard cells are sensitive to $CO_2$ concentration only from their inner side (i.e., concentration in the leaf interior). Stomata of a plant transferred to dark $CO_2$ free environment will remain closed but they will open in light when internal $CO_2$ is utilised.

**vii. Oxygen:**

It is essential for opening of stomata.

**viii. pH:**

Rise in pH is known to be required for opening of stomata while a fall in pH induces closure of stomata.

**ix. Growth Hormones:**

Cytokinins are essential for opening of stomata while abscisic acid takes part in stomatal closure.

**x. Minerals:**

Stomatal opening depends upon availability of $K^+$ ions from adjacent epidermal cells. A number of other minerals are also essential for stomatal movements, e.g., P, N, Mg, Ca, etc.