Chapter 2. WATER NUTRITION

1. The importance of water in plants

Water is a very important constituent of plants :

a. At cellular level: It is a liquid within which all metabolic reactions take place, and a diffusion medium for all ions and metabolites.

b. At plant level: Water is a fluid which circulates in the conductive vessels, forming the raw and elaborated sap with the matter in solution. It is responsible for the turgidity of all the cells.

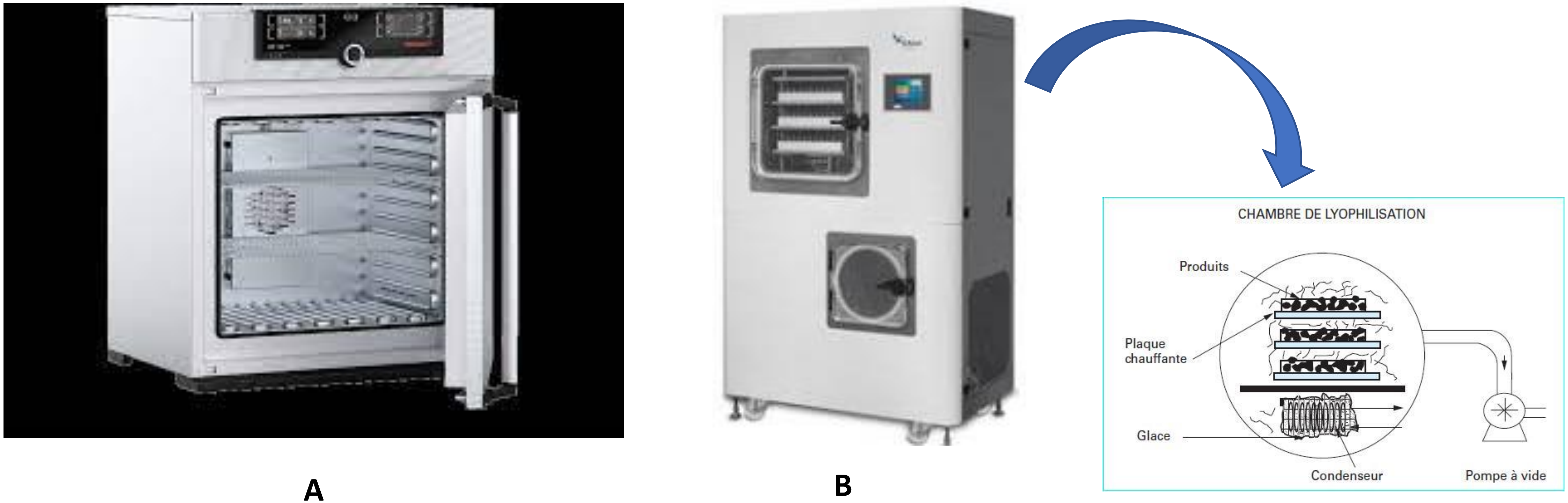
- The water content of plants :

To measure the water content of plants, the plant material is generally dried.

The quantity of water contained is given by the difference in weight between the fresh matter and the dry matter.

Drying method : Oven at high T° (70-110°C) and under vacuum until the material maintains a constant weight.

Cryodrying (cryodessication) or freeze-drying (Lyophilisation) (currently widely used).



A

B

Figure 1. Equipment - Drying methods
(**A.** Drying oven and **B.** Lyophilisation)

In plant cells, the vacuole is a reservoir of water. This water circulates within the plant, i.e. it passes through the sap-conducting vessels: **the xylem**, which carries the raw sap, and **the phloem**, which carries the processed sap.

The **water content** of a plant is given by the following formula:

$$\boldsymbol{\Theta = (Mf - Md)/Mf*100}$$

(ϴ (%) - Mf (fresh matter) - Md (dry matter))

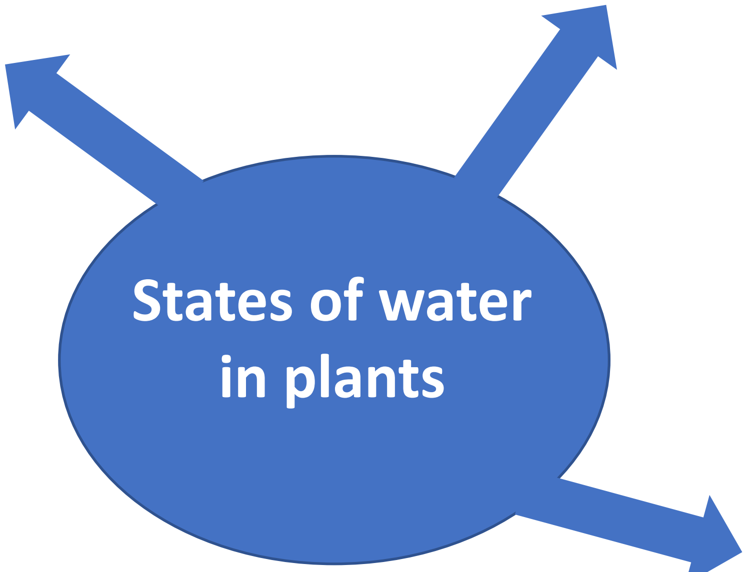
The **water deficit** is given by : $\mathbf{D\theta = (\Theta m - \Theta r)/\Theta m}$

ϴm (maximum content) and ϴr (real content)

- The state of water

1. Water bound by H bonds around alcoholic, amino or carboxylic groups (e.g. cellulose).

2. Free water: water circulating in plants or stagnant in vacuoles.



3. Water of constitution: plays a part in the stability of the structure of some protein macromolecules.

- The water molecule (H_2O)

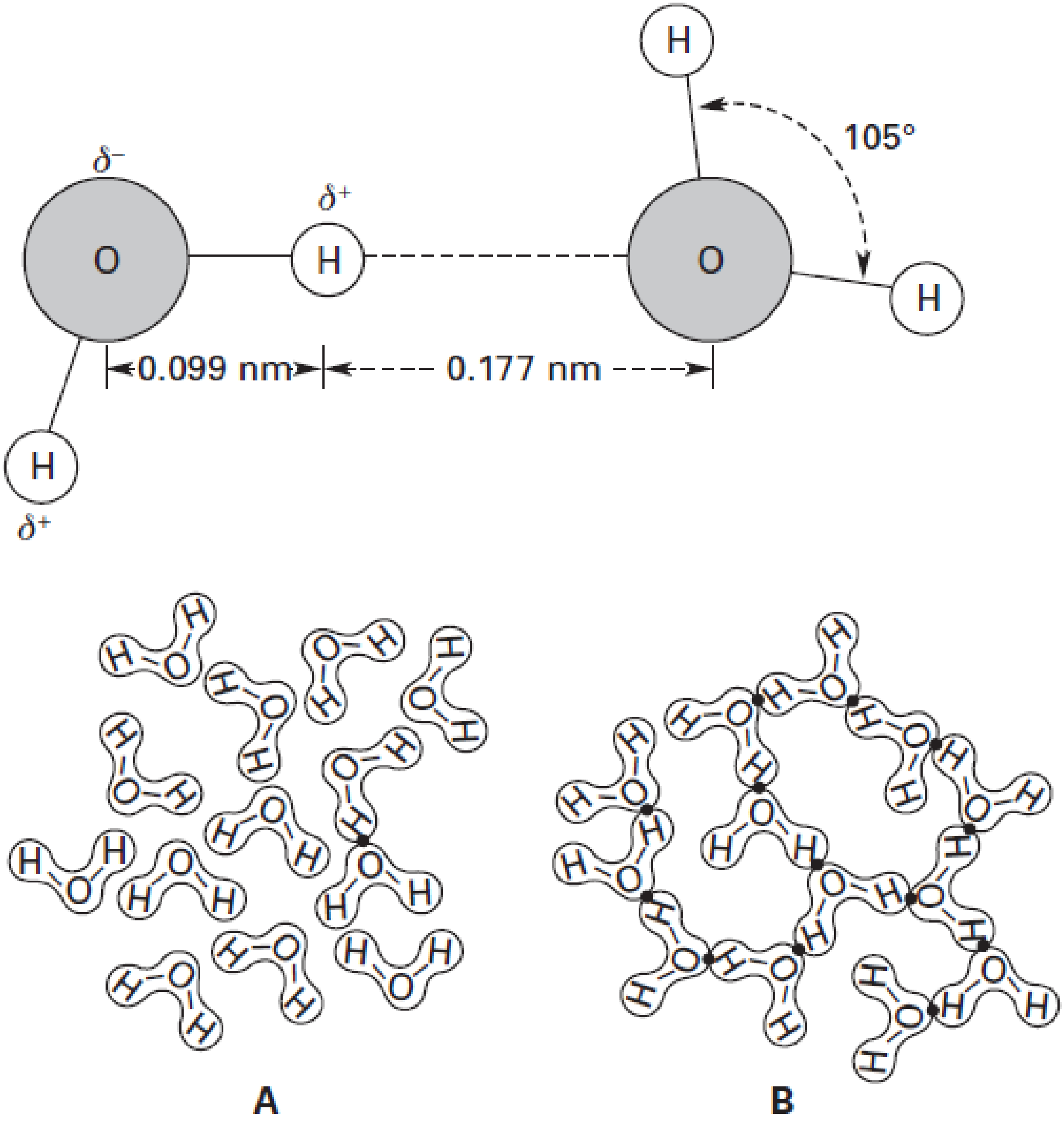
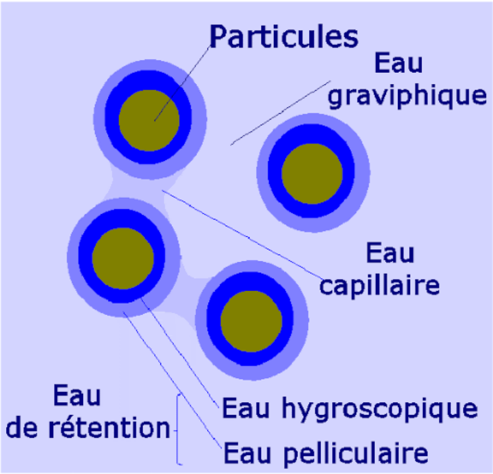


Fig. 2 Top section. Schematic diagram of 2 water molecules joined by an hydrogen bridge. This electrostatic bridge is based on the dipolar nature of the molecule: excess positive charge in the H; excess negative charge in the 0. The energy of the bridge is relatively lower (approximately 20 KJ/mol) than that of the covalent bond (approximately 400 KJ/mol). Lower part. Structure of water at (A) 100°C and (B) 0°C. H-bridges are indicated by black dots (Nobel 2004, Meidner and Sheriff 1976).

2. Water uptake by roots:

- **<u>Water in the soil.</u>** A soil may contain : free circulating water and water retained to a greater or lesser extent by capillary action in the small channels between the rocks, or by adsorption to the surface of the minerals (hygroscopic water), or water of constitution. The quantities of water immobilized in this way vary greatly from one soil to another.



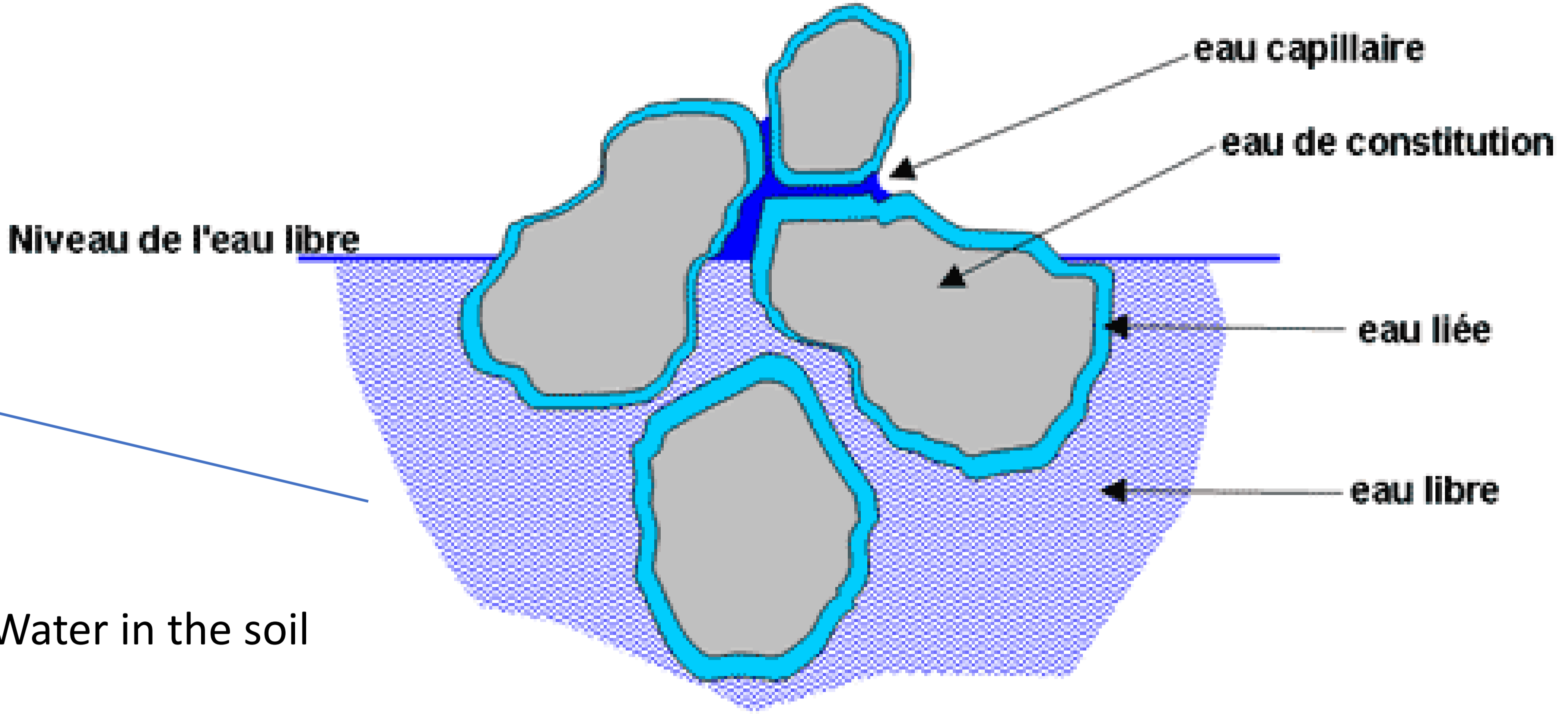


Fig. 3 Water in the soil

- The water content and rate of water movement in soils depend, to a large extent, on the **type** and **structure** of the **soil**. Soil water potential can be divided into 3 components:

1. **Osmotic potential (Ψs):** The water content of the soil is generally negligible.

2. **Hydrostatic pressure (Ψp):** Ψp is very close to zero for moist soils.

As the soil dries out, Ψp decreases and can become negative. As the **water content** of the soil decreases, water withdraws into the interstices between soil particles, forming air-water surfaces. As the soil dries out, water is first removed from the larger space between soil particles.

The value of Ψp can easily reach -1 to -2 MPa when the air-water interface recedes into the smallest spaces between the clay particles.

3. Gravitational potential (Ψg). Gravity plays an important role in drainage.

- **Water uptake by roots**

Contact between the root surface and the soil is essential for efficient water absorption. Absorbent root hairs **(Fig. 4)** are filamentous outgrowths of the root's epidermal cells and offer a greater capacity to absorb ions and water from the soil **(Fig. 5)**.

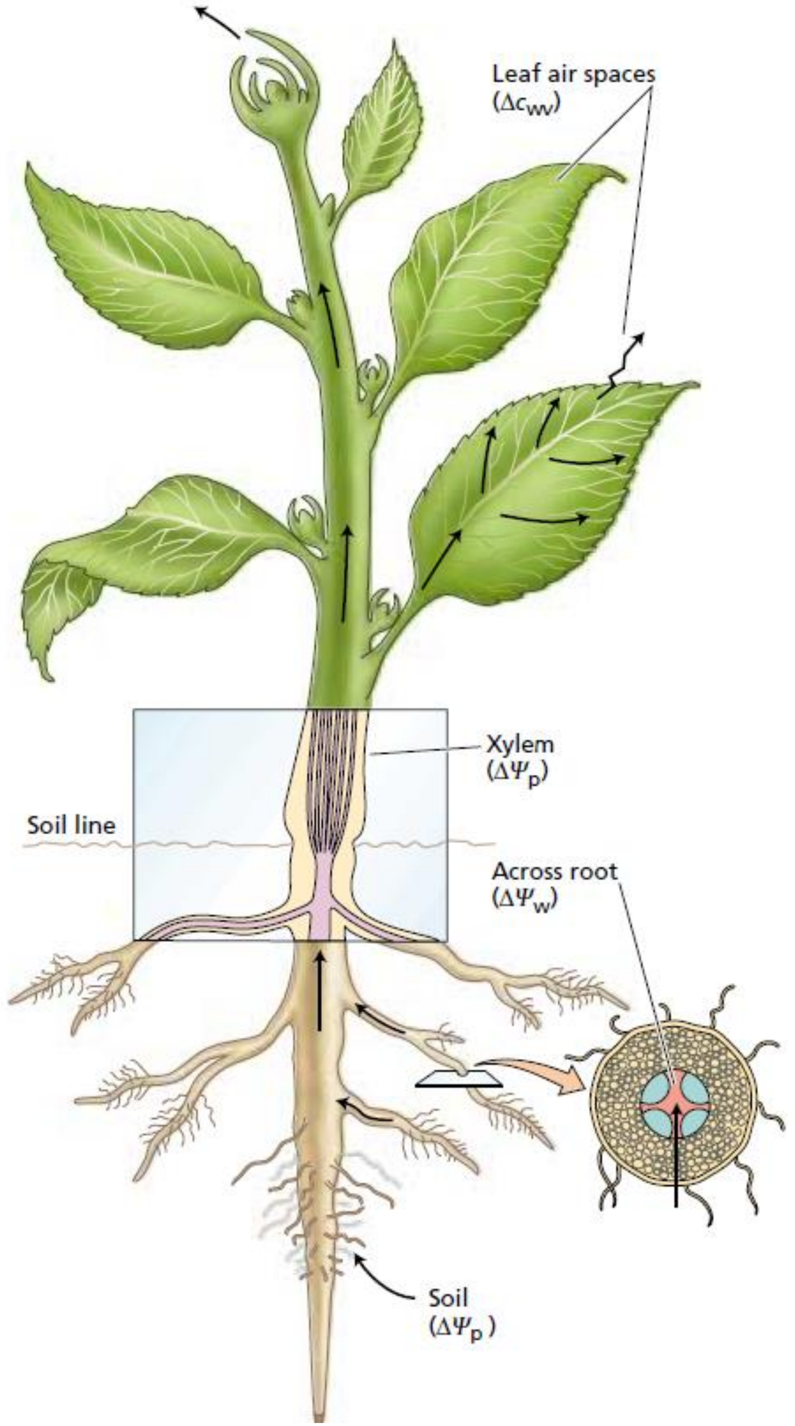


Figure 4. Absorbent root hairs.
(*source: Taiz L., Zeiger E., 2010*)

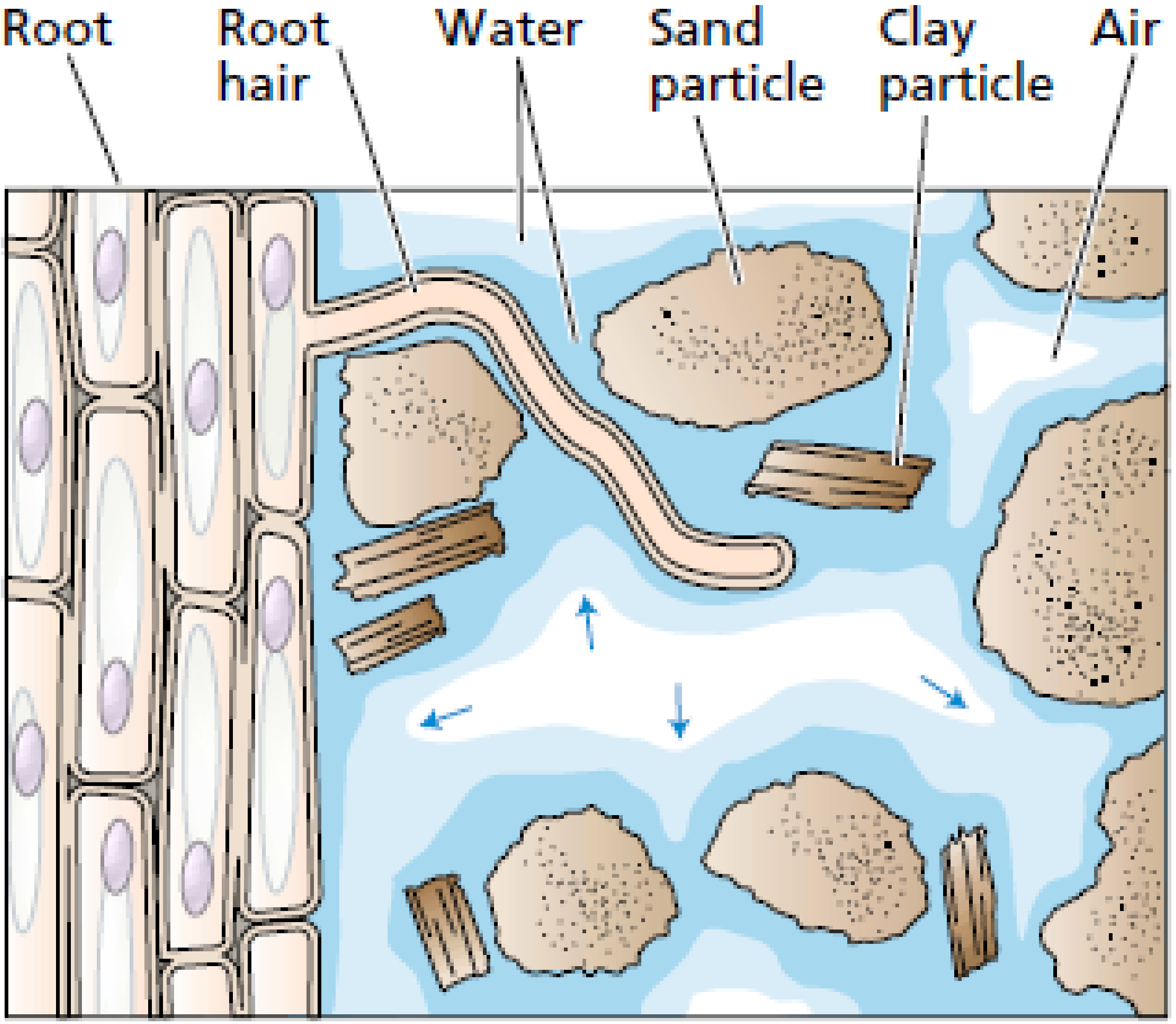


Figure 5. Contact entre la racine et le sol

(*source: Taiz L., Zeiger E., 2010*)

- Water movement in the root

There are **3 routes** by which water can flow from the epidermis to the endodermis of the root: the **apoplast**, the **symplast** and the **transmembrane route** **(Fig. 5)**.

-The apoplast: This is the continuous system of cell walls and intercellular air spaces. Water moves through the root cortex without passing through any membranes.

-The symplast: This is the entire network of cell cytoplasm interconnected by plasmodesmata. Water passes through the root cortex via the plasmodesmata (does not cross the plasma membrane).

-The transmembrane pathway: Water enters a cell on one side, leaves the cell on the other side and enters the next series of cells, and so on. The water crosses the plasma membrane of each cell twice on its way.

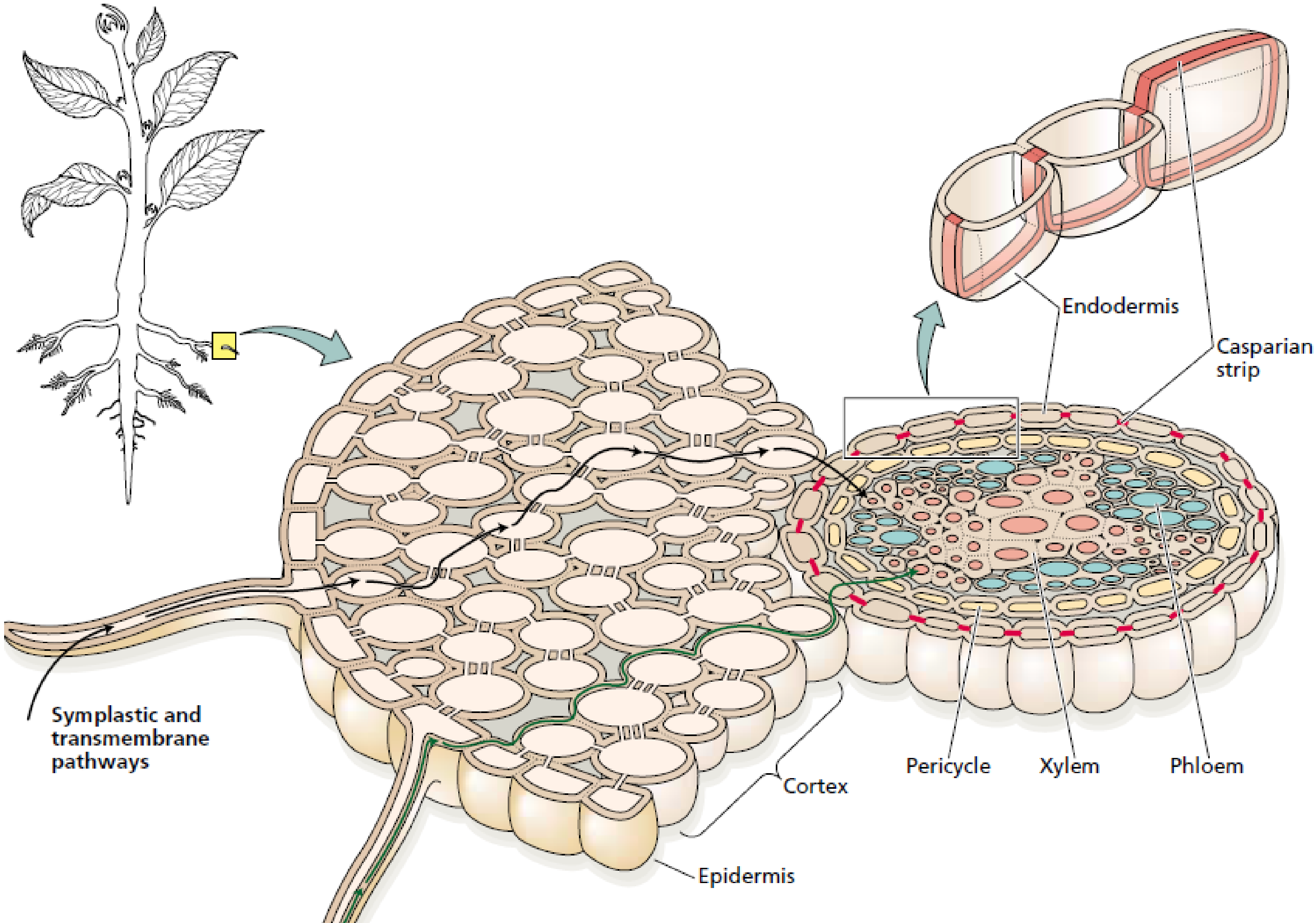


Figure 5. athways for water uptake by the root. Through the cortex, water may travel via the apoplast pathway, the transmembrane pathway, and the symplast pathway. In the symplast pathway, water flows between cells through the plasmodesmata without crossing the plasma membrane. In the transmembrane pathway, water moves across the plasma membranes, with a short visit to the cell wall space. At the endodermis, the apoplast pathway is blocked by the Casparian strip.

Note: In the **endodermis**, the Caspary band breaks the continuity of the apoplast pathway, forcing water and solutes to cross the plasma membrane into the endodermis. The requirement for water to move symplastically through the endodermis helps to explain why root water permeability is highly dependent on the presence of **aquaporins**.

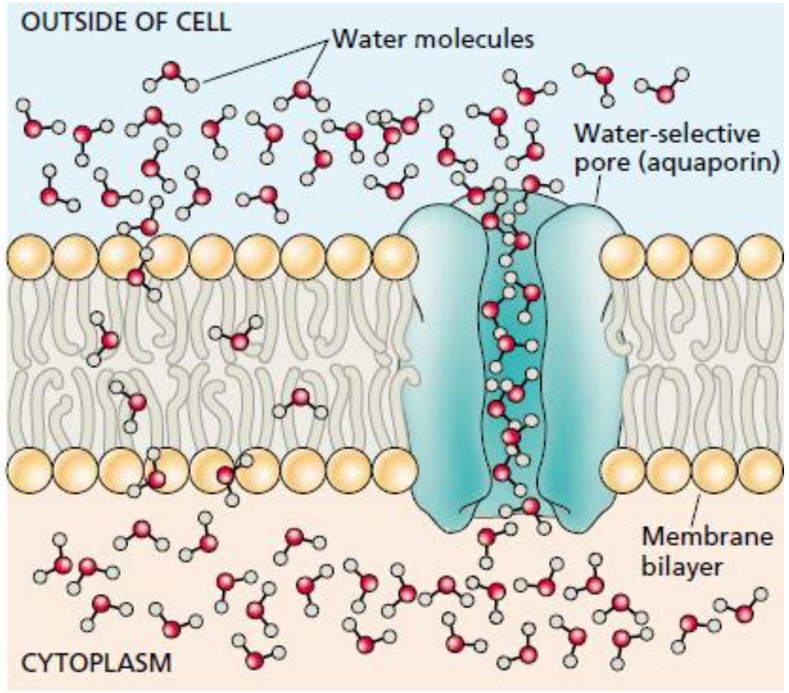
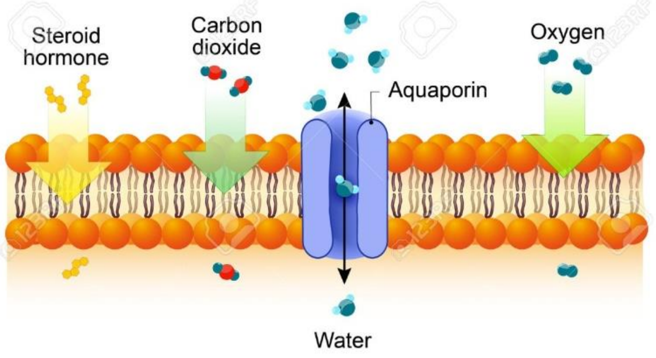


Figure 6. Water can cross plant membranes by diffusion of individual water molecules through the membrane bilayer, as shown on the left, and by microscopic bulk flow of water molecules through a water-selective pore formed by integral membrane proteins such as aquaporins.



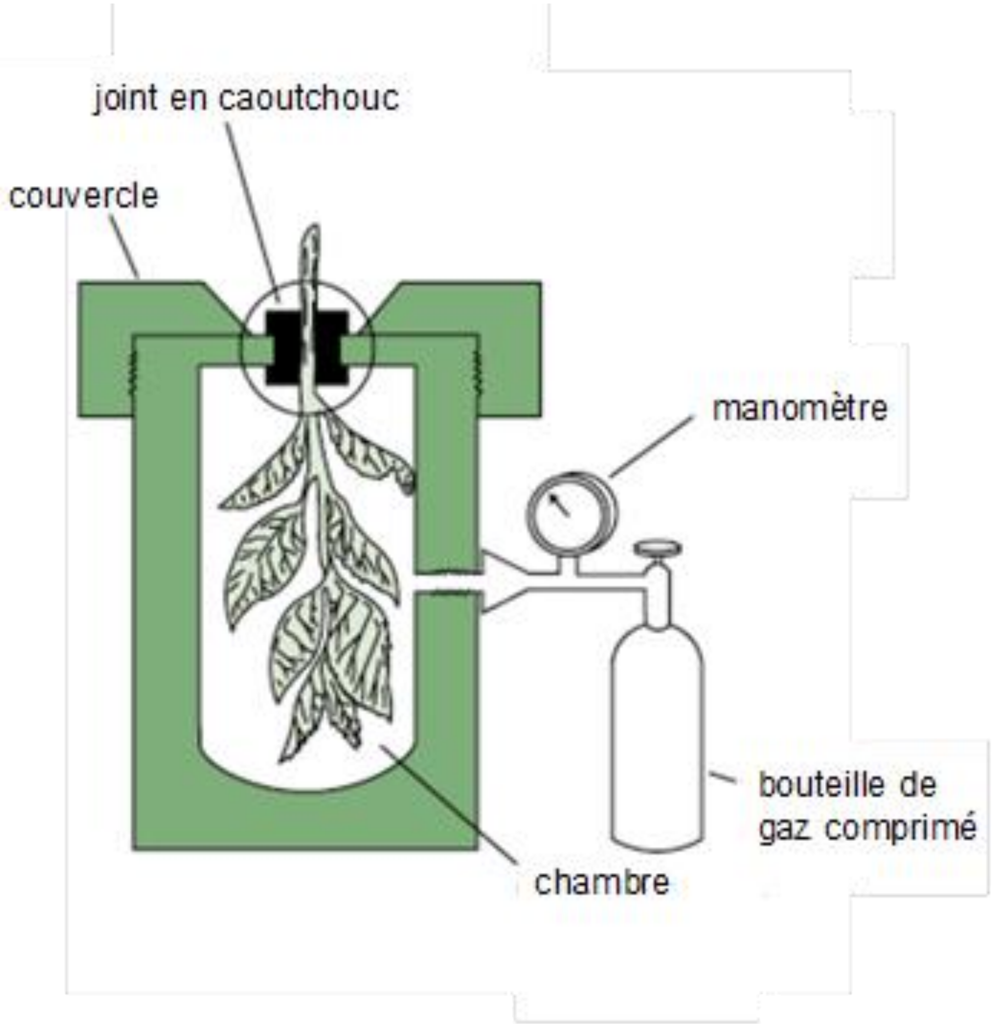
Water uptake decreases when roots are subjected to low-temperature or anaerobic conditions.

A **decrease in the rate of respiration**, in response to low temperatures or anaerobic conditions, can lead to an increase in intracellular pH. This increase in cytoplasmic pH alters the transport strength of aquaporins in root cells, resulting in roots that are significantly less permeable to water.

- Transport through xylem

Vascular tissues include xylem and phloem, which carry water and nutrients between the various organs. The **Xylem** tissue transports water and dissolved minerals from the root through the stem to the aerial organs. The **phloem** is responsible for transporting organic matter from sites of synthesis to sites of storage or sites of metabolic reactions.

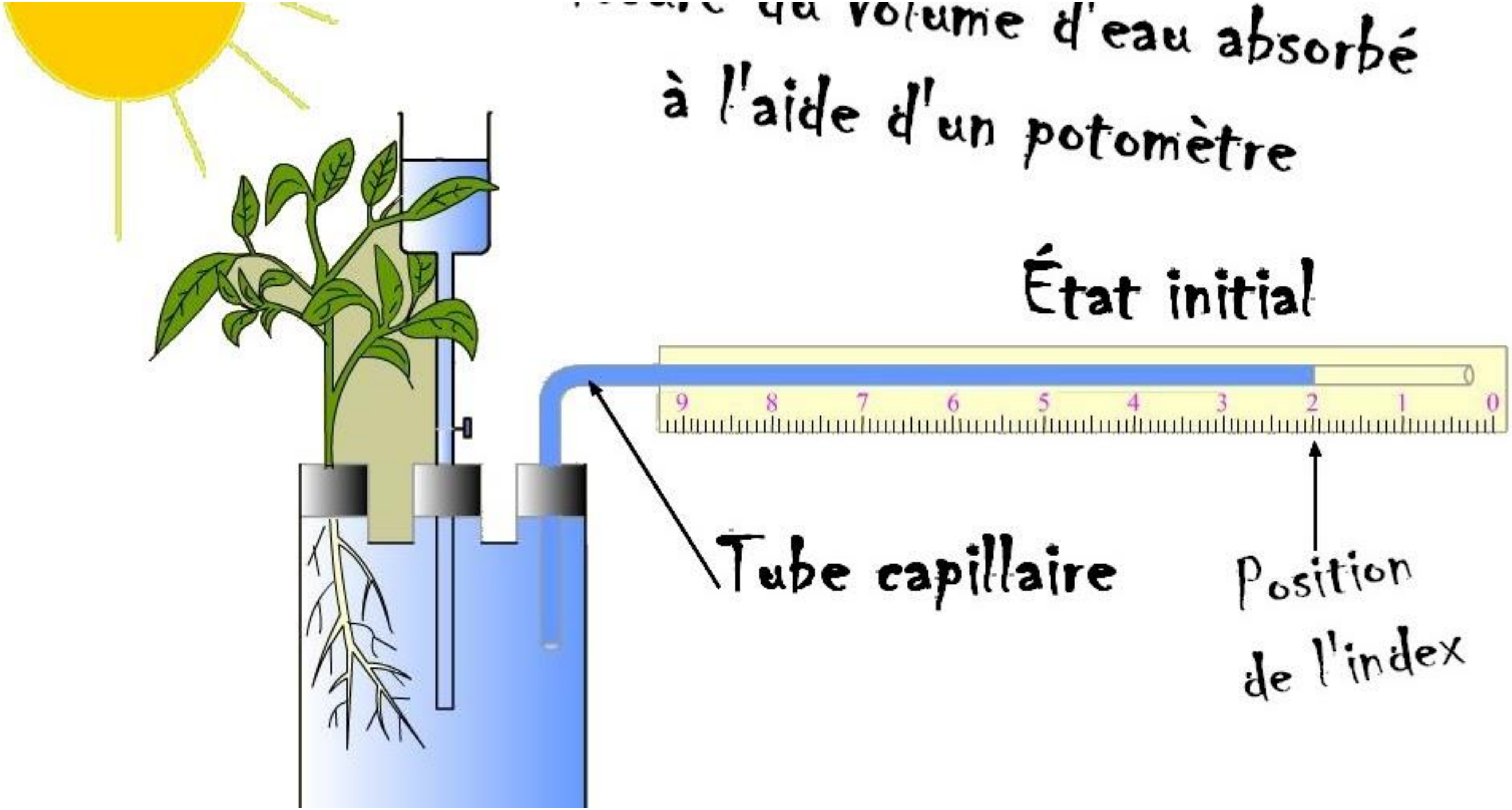
Experiment on the transport of **raw sap** in the xylem, using a pressure gauge: Plants sometimes exhibit a phenomenon known as root pressure. If the stem of a young plant is cut just above the ground, the stump often releases sap from the cut xylem for several hours.



3. Methods for measuring water uptake by roots :

A priori, it is assumed that the quantity of water absorbed is equal to the quantity of water lost through transpiration. This estimate neglects the quantities of water transformed or produced by metabolism, which are very small compared with the enormous masses of water circulating through plant organisms.In the soil, the quantity of water drawn off by a plant can be measured by ;Simple weighing A potometer

du volume d'eau absorbé
à l'aide d'un potomètre



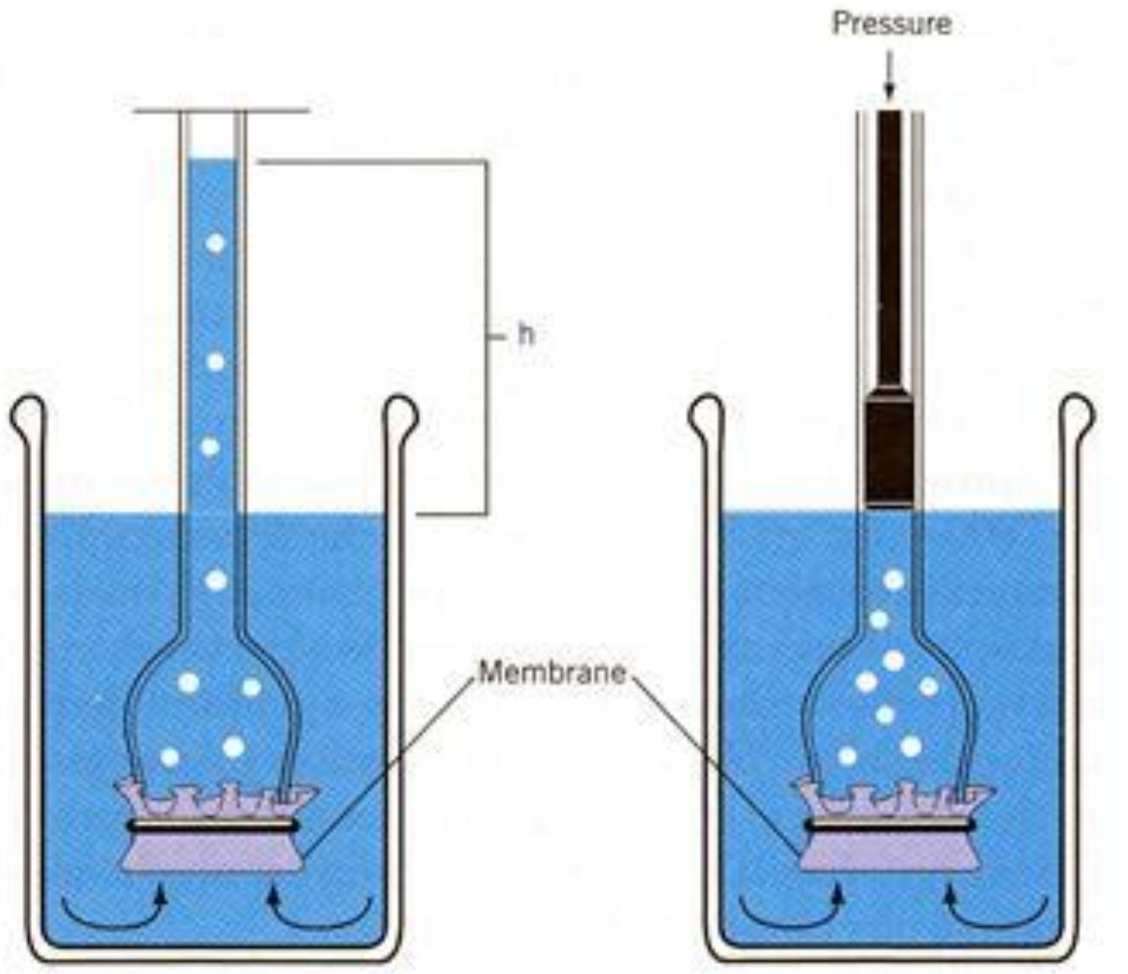


Figure 1: Hydrostatic pressure demonstration
(*source: Hopkins W.G., Hüner N.P.A., 2009*

- The concept of water potential

The concept of water potential was introduced in 1960 by R.O. Slatyer and S.A. Taylor, as a measure of the free energy of water per unit volume (J m-3).

These units are equivalent to units of pressure such as the pascal, which is the common unit of measurement for water potential.

The main factors influencing **plant water potential** are concentration, pressure and gravity. Water potential is expressed by Ψw (the Greek letter psi)

The water potential of solutions is: $\Psi w = \Psi s + \Psi p + \Psi g$

Water Potential and Its Components

Chemical potential is a relative term expressed as the **difference between the potential of a substance in a given state and the potential of the same substance in a standard state**. The chemical potential of water (plant physiologists use the term water potential) is the free energy of water. It is the chemical potential of water divided by partial molar volume. In terms of pressure units, water potential is expressed as MPa (megapascal). The lower the water potential of the plant, the greater is its ability to absorb water and vice versa. Water potential is not an absolute value and is symbolized by the Greek letter Ψw (psi). Water potential of pure water is maximum and its value is zero at the atmospheric pressure. **In a living cell, water potential refers to the sum of the following components : Ψw = Ψs + Ψp + Ψm + Ψg**

where Ψw is the water potential, Ψs solute/osmotic potential, Ψp pressure potential, Ψg gravitational potential, and Ψm matric potential.

Osmosis can be easily demonstrated using a device called an osmometer. The volume of the solution will continue to increase until the **hydrostatic pressure** developed in the osmometer tube is sufficient to balance the force driving the water in the solution. This force is known as **osmotic pressure**.

Osmotic potential is the negative of osmotic pressure, because they are equal but opposite forces. Positive pressures increase the potential of water; negative pressures reduce it. The positive hydrostatic pressure inside the cells is the turgidity pressure.

Negative hydrostatic pressure (tension) develops in the xylem and in the walls between the cells. Gravity causes the water to sink unless it is opposed by an equal and opposite force. The term Ψg depends on the height (h) of the water above the water reference state.

The **Ψg** of the water potential is usually omitted from considerations of water transport at the cell level. Thus, in these cases, the equation can be simplified as follows: **$\Psi w = \Psi s + \Psi p$**

Water potentials can be measured by various methods, such as the Sholander pressure chamber (Figure). In this technique, the organ to be measured is excised from the plant and partially sealed in a pressure chamber. Before excision, the water column in the xylem is under tension.

When the water column is broken by excision of the organ (i.e. its tension is relieved, allowing its ΨP to rise to zero), water is rapidly drawn from the xylem into the surrounding living cells by osmosis. As a result, the cut surface appears dull and dry. To make a measurement, the operator pressure rises the chamber with compressed gas until the distribution of water between the living cells and the xylem ducts returns to its initial state before excision. This can be seen visually by observing the return of water to the open ends of the xylem ducts, which can be seen in the cut surface.

The pressure required to return the water to its original distribution is called the equilibrium pressure and is easily detected by the change in appearance of the cut surface, which becomes moist and shiny when this pressure is reached. Pressure chamber measurements provide a quick and accurate method of measuring leaf water potential. As the pressure chamber method does not require sensitive instrumentation or temperature control, it has been widely used in the field.

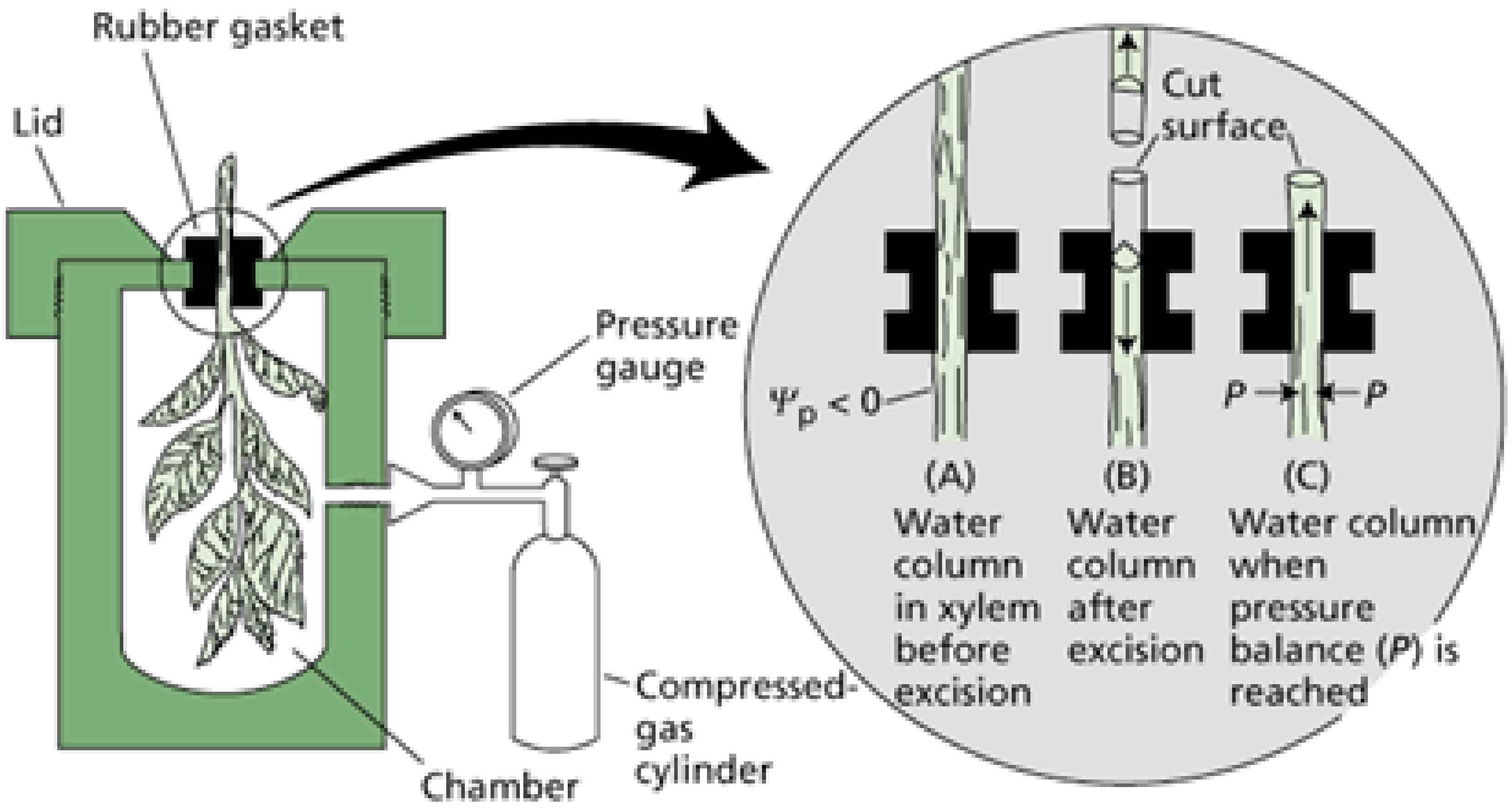


Figure . Pressure chamber method (*source: Taiz L., Zeiger E., 2010*).

3. Mechanisms of absorption:

The concept of osmotic pressure : The fluid in the vacuole of a plant cell has a certain level of osmotic pressure.

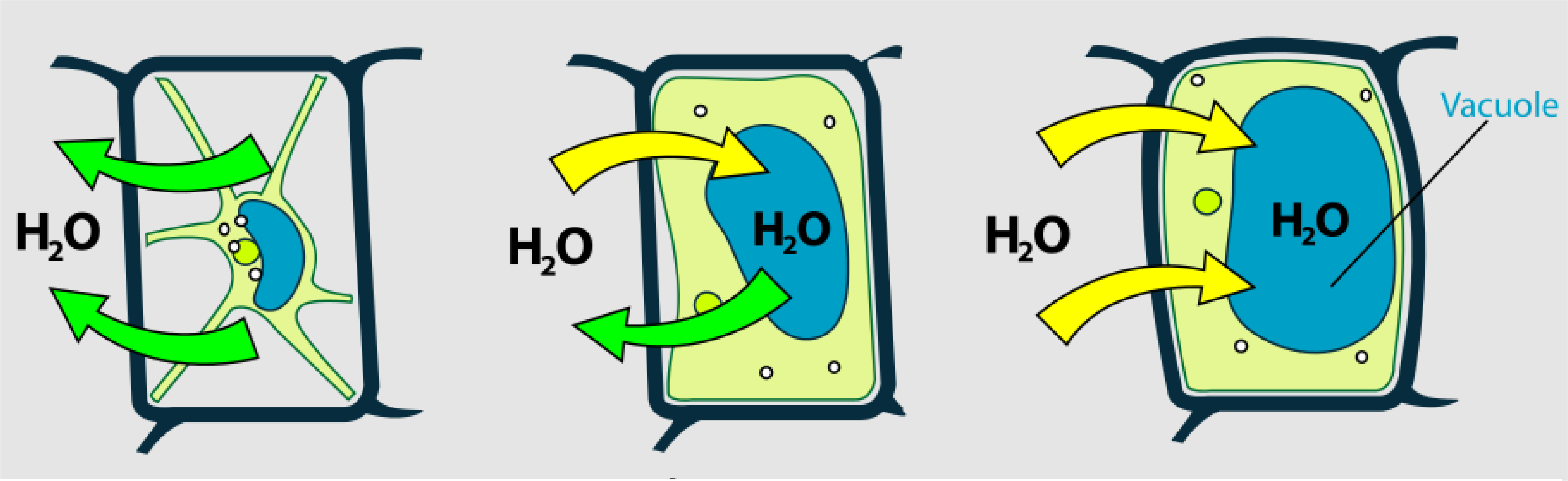
$$\mathbf{P\ osm = R.T\ C = 22.4\ C \qquad \text{à} \quad 0°C}$$

P osm : Osmotic pressure
R : Constant of perfect gases
T : Absolute temperature
C : Molar concentration of the vacuolar liquid

Cellular mechanisms of absorption at the root level Water is always absorbed through a cell wall. To explain the mechanisms of absorption: The exchange of water between the intracellular and extracellular medium takes place across the cytoplasmic membrane according to the physical laws of diffusion: **osmosis always occurs from the hypotonic to the hypertonic medium.**

A cell placed in a solution that is hypertonic with respect to the intracellular medium loses water and becomes **plasmolysed**. If, on the other hand, it is placed in an extracellular medium that is hypotonic with respect to the intracellular medium, water enters the cell and the vacuole swells : the cell is then swollen (see Fig.)

Hypertonic | Isotonic | Hypotonic



Plasmolysed cell | Equilibrium | Turgid cell

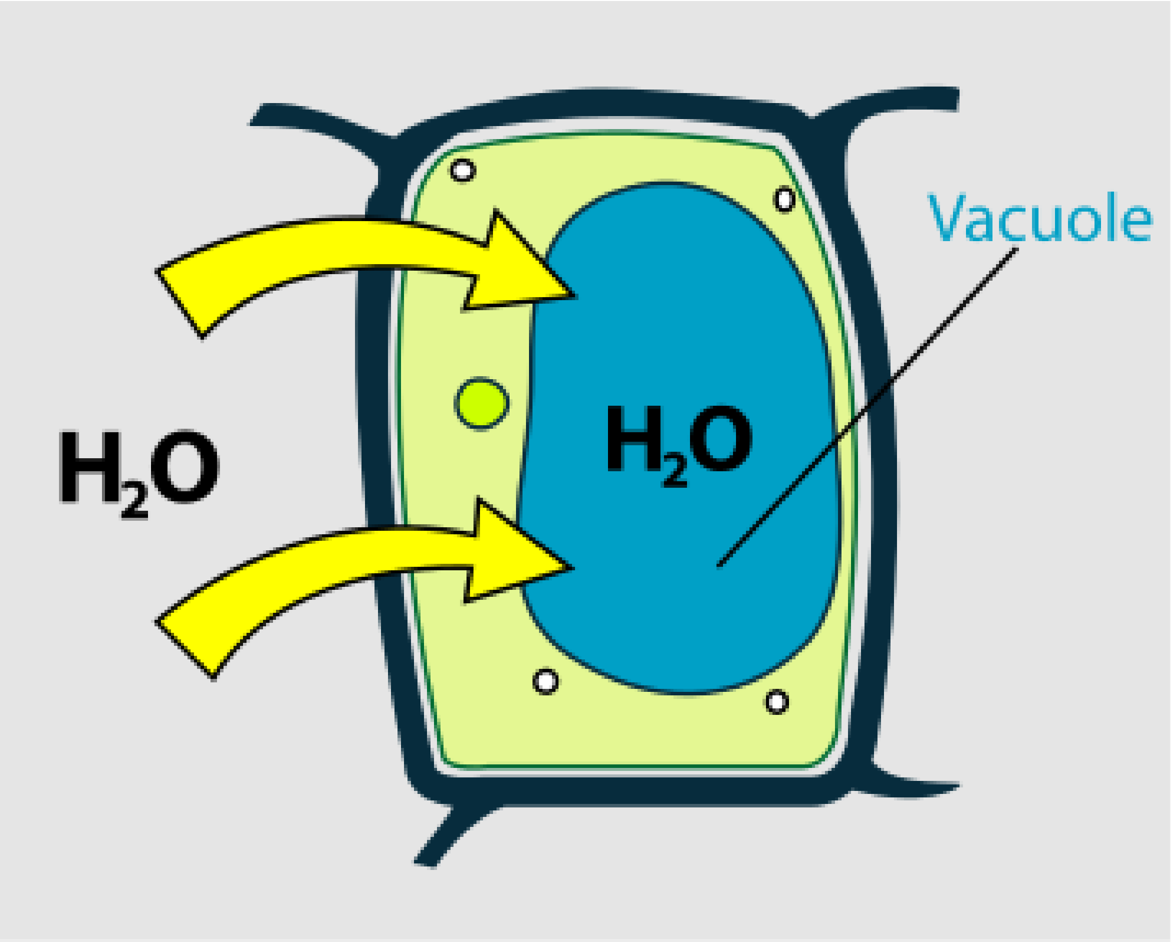
Under natural conditions, the absorbing hair cell is always hypertonic in relation to the soil solution: it therefore absorbs water passively by osmosis.

A plant watered with a solution that is too concentrated in mineral salts will wither and die because the root cells not only stop absorbing water, but also lose it, leading to plasmolysis.

Hypotonic state :

In a hypotonic medium (osmotic pressure of the medium < osmotic pressure of the vacuolar fluid of the cell) : Water moves from the least concentrated medium to the most concentrated medium (the cell). The cell therefore swells and becomes distended: The cell wall expands under the effect of this osmotic pressure (Posm) and opposes a membrane pressure (Pmbr) against it (Posm) until equilibrium is reached or the cell achieve its maximum volume.

Hypotonic medium : Turgid cell

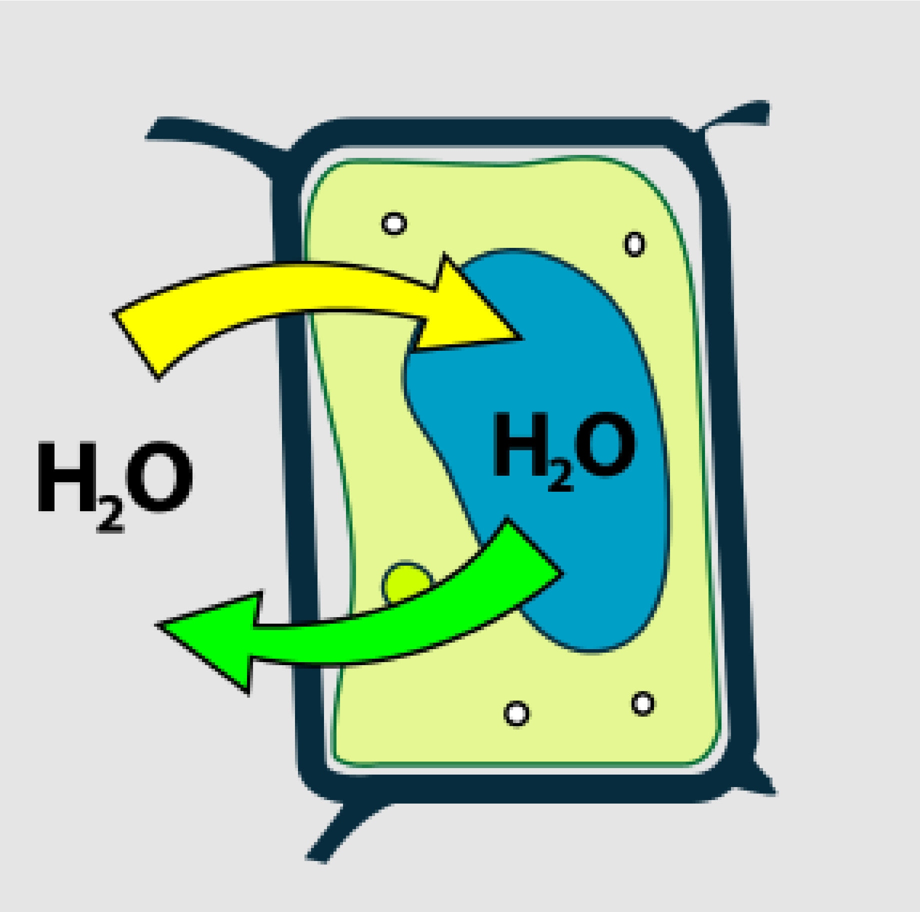


Isotonic state :

An isotonic solution with respect to the intracellular medium contains an amount of dissolved solutes equal to that of the cytoplasm. The osmotic pressure of the vacuolar fluid decreases to oppose the resistive pressure of the pectocellulosic wall until equilibrium is reached. This is the "suction S" force, obtained by the difference between the osmotic pressure and the membrane pressure.

$$S = Posm - Pmbr$$

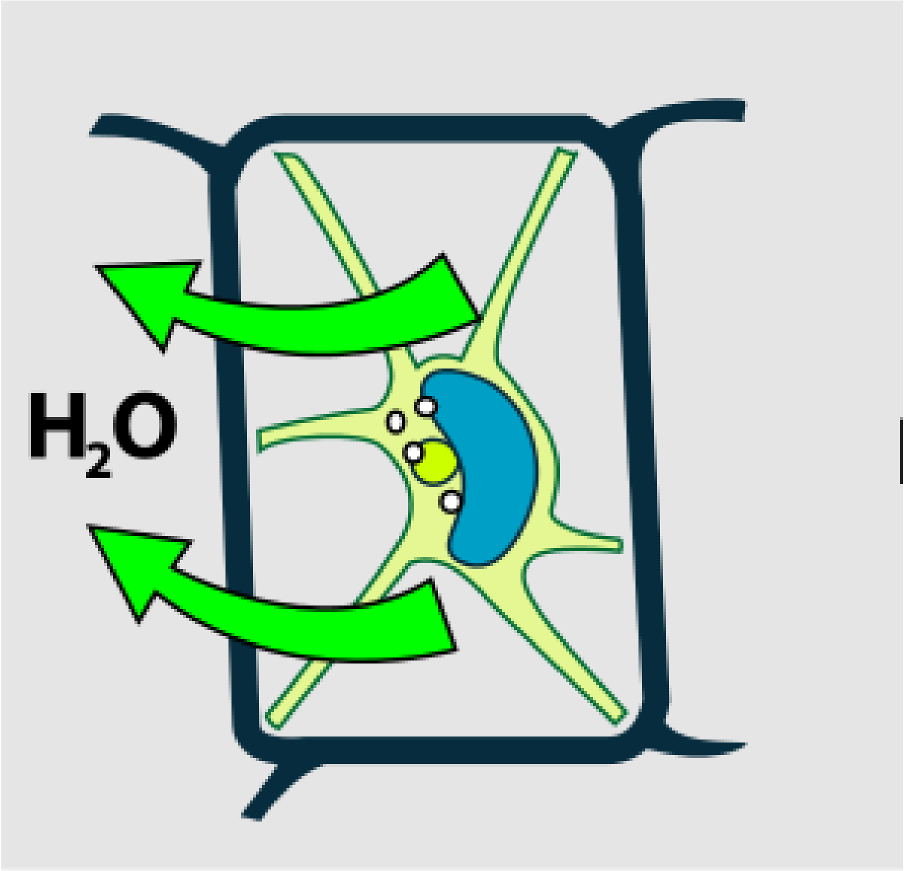
Isotonic state : Equilibrium



Hypertonic state

If the medium has a lower water suction force than the cell, water will leave the cell to the outside, causing plasmolysis of the cell; In other words, the vacuole of the absorbing hair must be sufficiently hypertonic with respect to the soil solution to overcome the resistance to water entry caused by turgidity.

Hypertonic state : plasmolyse cell



4. Transit of water in the plant :

a. ROOTS :

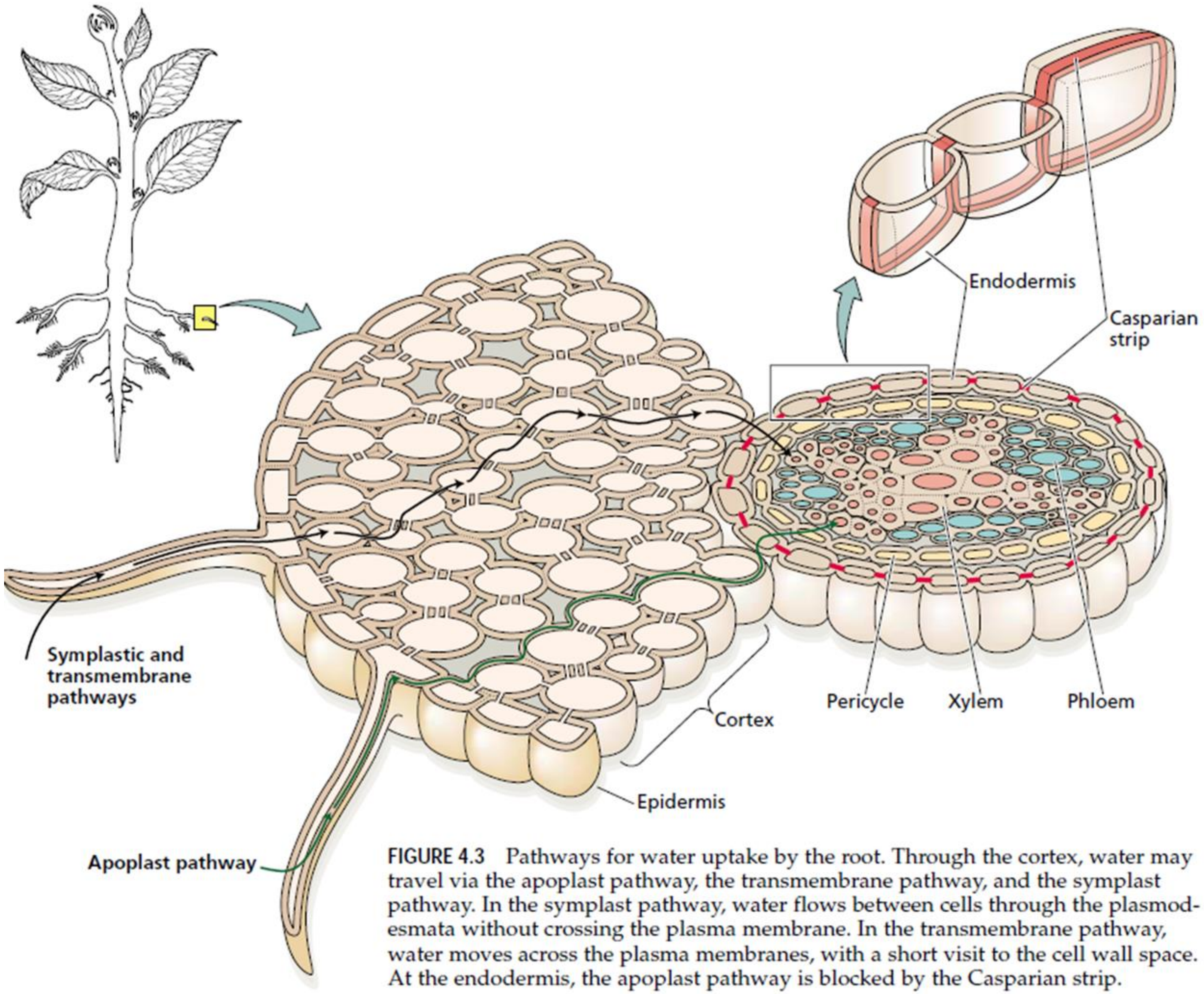
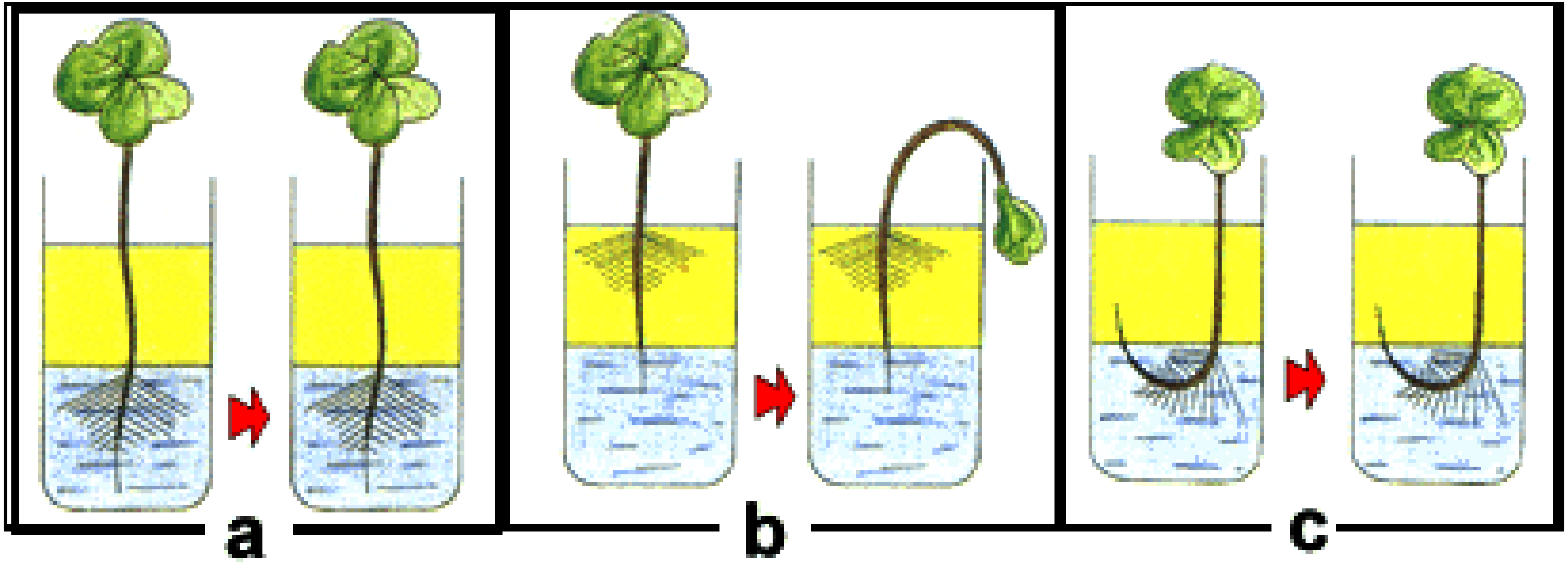


FIGURE 4.3 Pathways for water uptake by the root. Through the cortex, water may travel via the apoplast pathway, the transmembrane pathway, and the symplast pathway. In the symplast pathway, water flows between cells through the plasmodesmata without crossing the plasma membrane. In the transmembrane pathway, water moves across the plasma membranes, with a short visit to the cell wall space. At the endodermis, the apoplast pathway is blocked by the Casparian strip.

Experiment : In this picture you can see that the **absorbing hairs** are responsible for the **water uptake**.



Oil : Yellow color
Water : Bleu color

<u>Osmotic pressure measurements</u> on a **root** indicate the presence of an **inversion of the osmotic pressure gradient** in the **endodermis**. Water passes through the absorptive hairs and circulates **passively** according to the laws of <u>osmosis</u>, but from the endodermis onwards it requires an expenditure of energy :

active transport (see figure)

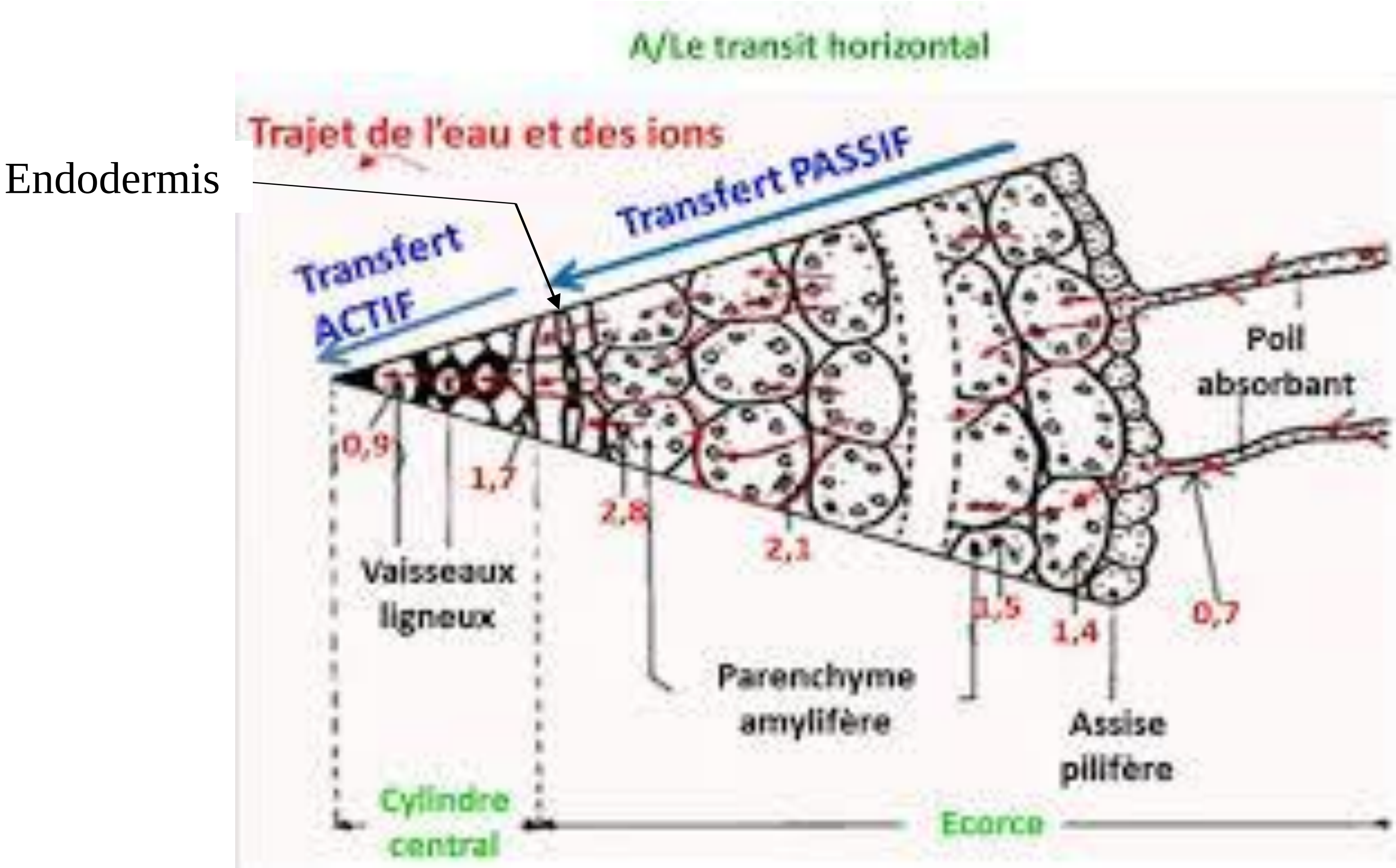


Figure : Water pathway from the absorbent hair to the root endodermis.

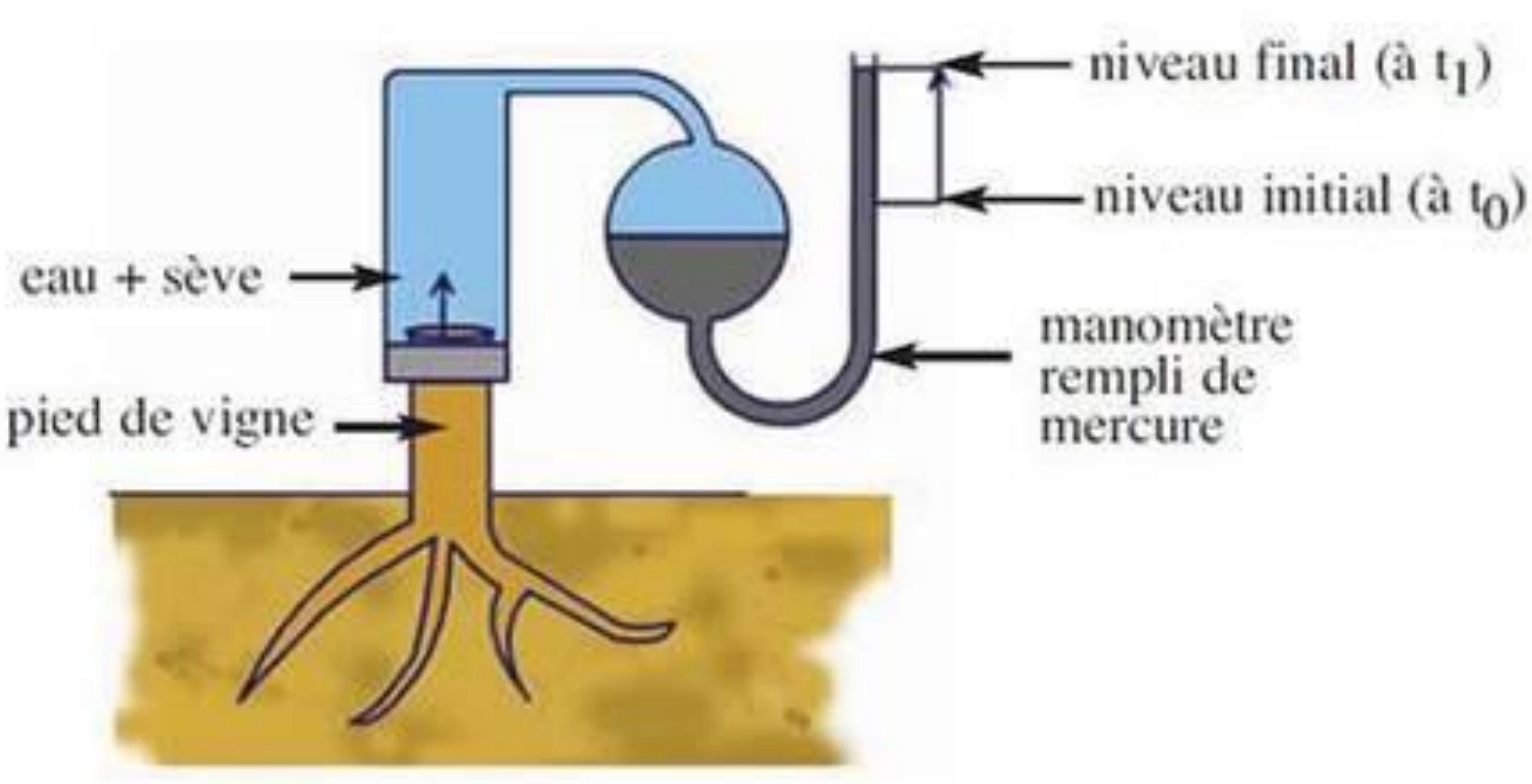
Water pathways: Water entering through the absorbent hairs reaches the conducting vessels via the cortex (bark) and the stele (central cylinder). It follows 3 routes :

-The **apoplasm**: all the cell walls, lacunae and meat, which are highly accessible to water and mineral ions.

-The **symplasm**: all the cytoplasm connected by junction systems such as plasmodesmata.

-The **transcellular transport**: (Vacuole to vacuole), through cytoplasmic walls and layers; this transport is called transcellular transport

Root pressure: Water is released under pressure at the entrance to the containers; this is the **root pressure**, which often exceeds 1 bar (see figure)..



Mechanisms of root expansion: Under normal conditions, the movement of water in the root is due to transpiration. The mechanism of root thrust (or root pressure) is an active process linked to metabolism and several hypotheses have been proposed to explain it:

- The current trend is to assume that root pressure is largely osmotic in nature.
- There is an active secretion of ions into the conducting vessels, with the secreted ions removing water. This view is consistent with the fact that the salt concentration of raw sap follows a rhythm similar to that of root thrust.

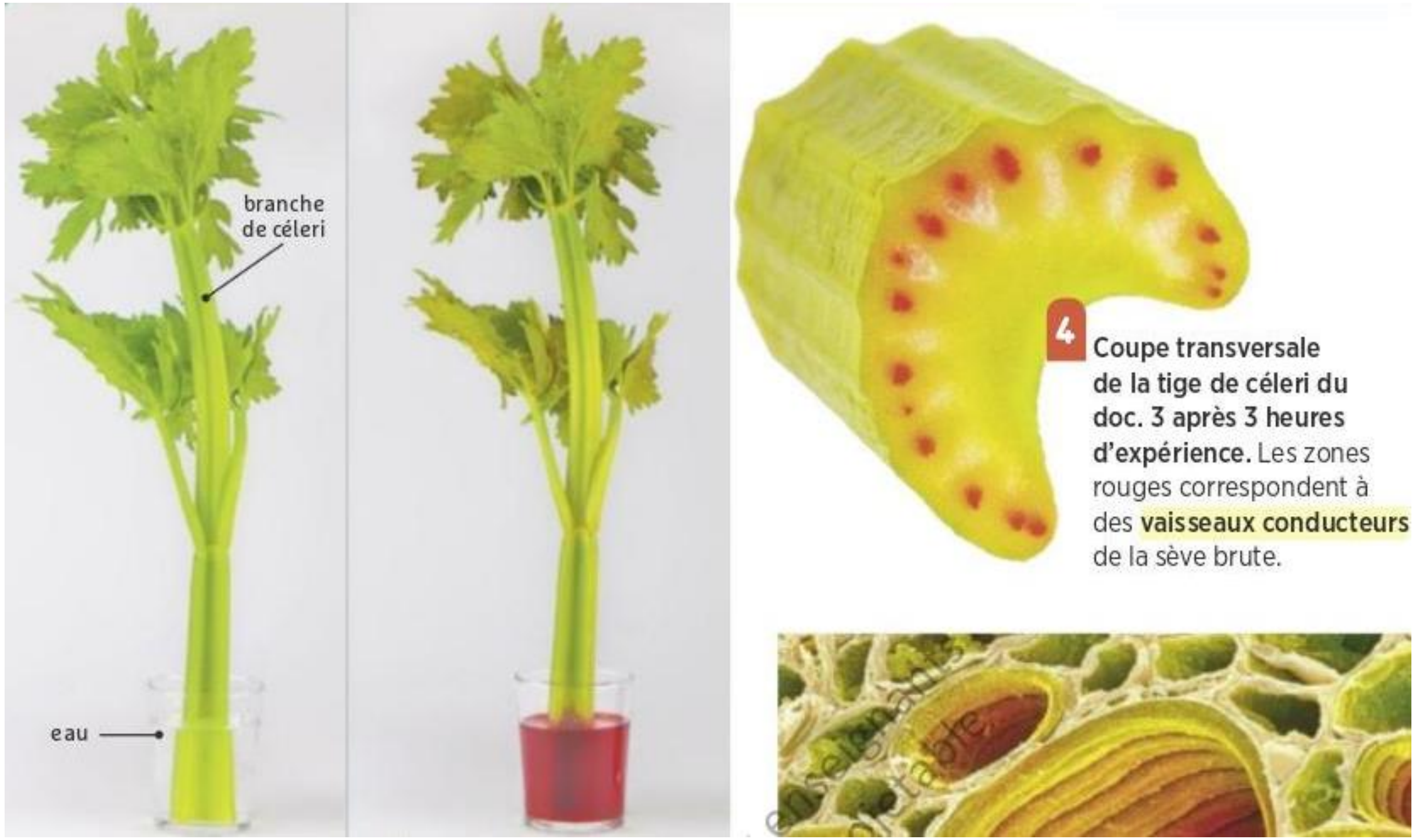
- The current trend is to consider root turgor to be largely osmotic in nature.

- There is an active secretion of ions into the conducting vessels by the cells of the stele, and the secreted ions carry the water away. This view is consistent with the fact that the salt concentration of the raw sap follows a rhythm more or less similar to that of the root turgor.

b. In the stem:

The mineral solution coming from the cortex and collected in the vessels constitutes the raw sap, which is a very dilute solution of mineral salts (0.1 to 2 g/l) with an osmotic pressure of at least 1 bar, plus amino acids resulting from the reduction of nitrates in the roots. This solution will be poor in mineral salts but rich in organic substances (especially in spring when reserves are mobilized).

An experiment about the movement of the red solution in the vessels conducting the raw sap (xylem) from the cup (see picture).

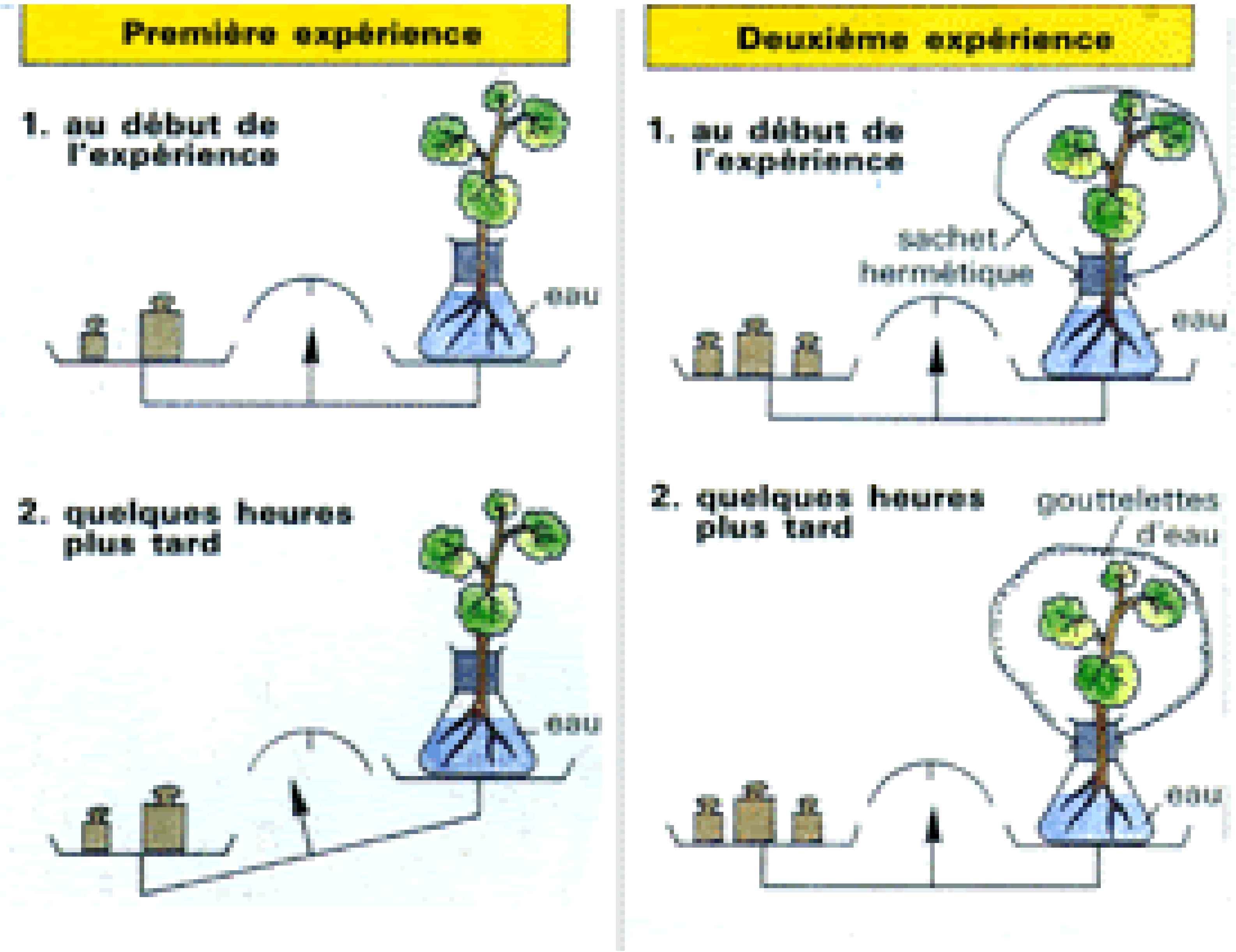


5. Transpiration :

Any deficit of water vapour saturation in the atmosphere surrounding a plant leads to a continuous evaporation of water: this is the **phenomenon of transpiration**, which creates a continuous demand for water in the plant and is the main driving force behind the ascension of the plant's sap.

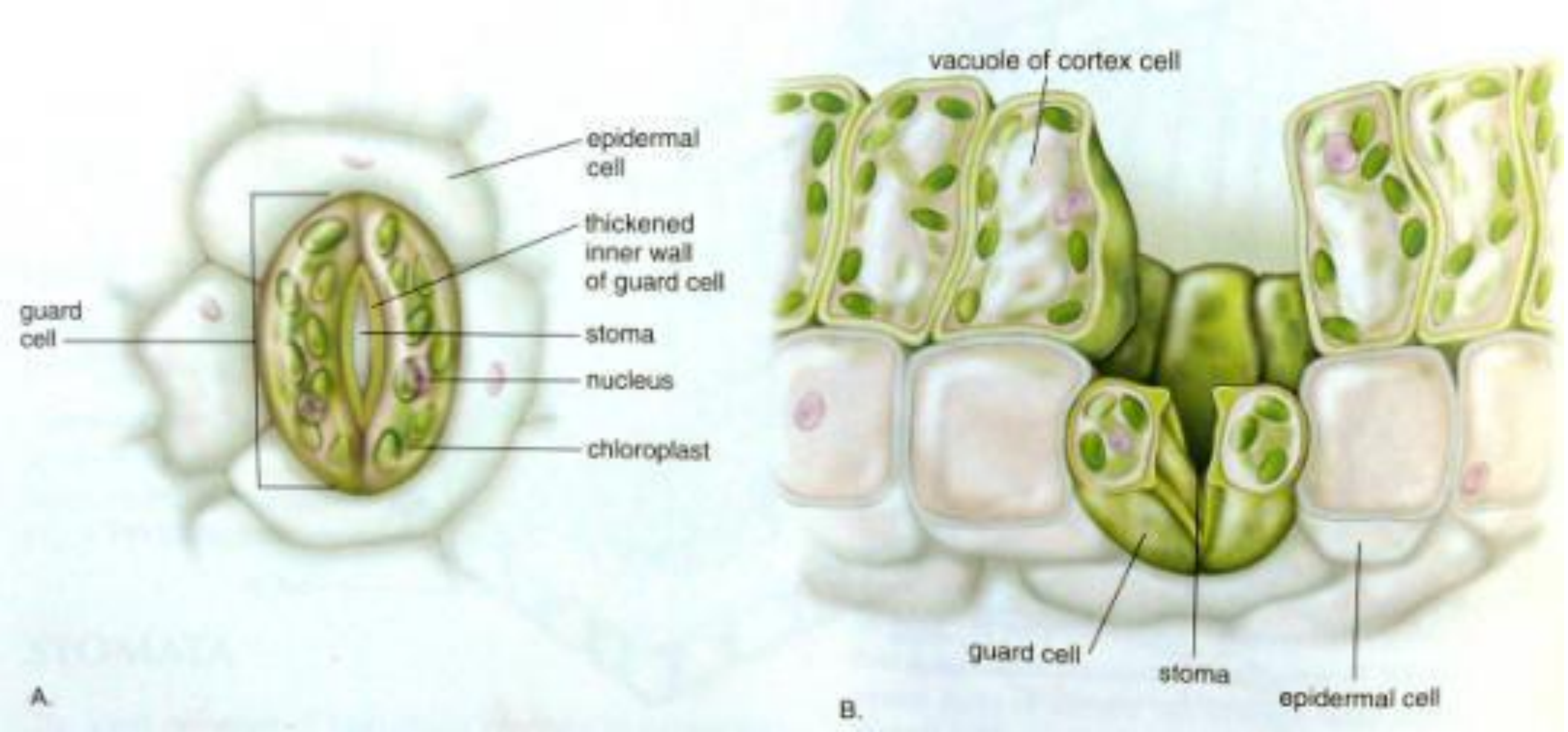
- For a plant, transpiration results in significant water requirements (if transpiration is too intense) and causes the plant to wilt and slow down its general metabolism.
- Wilting that is too advanced becomes irreversible, so transpiration is a potential danger to the plant.
- Transpiration can be overcome by anatomical devices and regulatory systems, such as the degree of stomatal opening, to adapt to very dry climates.

- Experiment related to the phenomenen of transpiration :



- Localization of transpiration at plant level

- Transpiration is mainly produced by leaves, young stems and flower parts. The lower epidermis of most plants generally resembles the upper epidermis, but the lower is perforated by numerous tiny pores called stomata. Some plants (e.g., corn) have these pores in both leaf surfaces, while others have them exclusively on the upper epidermis.
- Each pore is bordered by two sausage-shaped cells that usually are smaller than most of the neighboring epidermal cells. These guard cells are part of the epidermis, but they, unlike most of the other cells of epidermis, contain chloroplasts.
- The functioning of guard cells is aided by the photosynthesis that takes place within them. The primary functions include regulating gas exchange between the interior of the leaf and the atmosphere. When the guard cells are inflated, the stomata open;
- when the water content of the guard cells decreases, the cells deflate and the stomata close (See the following figures).



Melikyan Yelena (2017)

- Mechanisms of stomatal opening

Stomatal transpiration varies according to the opening and closing of stomata, which is linked to differences in osmotic pressure in the guard cells. The guard cells (and therefore the stomata) open or close according to osmotic forces corresponding to changes in the concentration of intracellular potassium. An increase in potassium concentration leads to the formation of an hypertonic medium, which causes the guard cells to turgidity and the stomata to open.

The guard cells have reinforced walls on the inside, which delimit the ostiole, and are often accompanied by epidermal companion cells, which lack chloroplasts, with which they are in close contact on their outer surface, allowing greater intercellular exchange.