

WATER RELATIONS IN PLANTS

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Summary

Water is an essential element for all living things. It is needed as a solvent, and all biochemical reactions of metabolic events take place in aqueous surroundings. Plants are no exception to this rule. They take up water from the soil through their root hair cell walls and plasma membrane channel proteins, and transport it in the xylem of vascular bundles up through the stem to the leaves, where most of it evaporates in the air. The flux of water is maintained by the water potential of the cells. This consists of several partial potentials. These transport events are described, as well as various environmental facts that affect the water status of the plant. The stomatal action and the importance of the cuticle on the epidermis are described, as well as the meaning of mycorrhiza and root nodules on nutrient and water uptake by the roots. The transport of water and organic solutes, and factors affecting this transport is also discussed.

1. Importance of Water to All Living Beings

Water is an essential element for all living beings. Most biochemical reactions of metabolic events take place in aqueous solutions and water also affects the structures of many organic molecules, such as proteins, nucleic acids, and polysaccharides. While in most cases water is needed as a solvent, it also participates in many biochemical reactions, such as hydrolysis and dehydration.

Water is also needed for the transport of nutrients and organic compounds and, for example, for the maintenance of a reasonable temperature in leaves under strong sunlight. For every gram of organic matter produced by the plant, approximately 500 g of water is taken up by the roots, transported through the plant, and eventually evaporated from the leaves to the atmosphere. Since plants have to keep their stomata open during daytime to allow the diffusion of CO₂ into the leaves for photosynthesis, plants are exposed to the hazards of drying through transpiration. This is why roots have to take up water constantly from the soil. The water, which is transported in the stems up to the leaves, is also used in the transport of nutrients to all parts of the plant. However, it has been shown that this transport with the flow of water is not of vital importance, and may affect only the major elements, such as potassium. Many plant species grow happily and transport nutrients to the leaves even in near 100% relative humidity, when transpiration does not draw water through the plant. Transport under this kind of experimental conditions is achieved through diffusion and mass flow (which will be explained later).

Plant cells and tissues, unlike animal cells, contain large amounts of cell wall material. This gives special features to plants. They do not need the support of a skeleton, but the more or less rigid cell wall material supports each cell. In cases where the cell wall is thin (e.g. in *Busy Lizzie* (*Impatiens* sp.) stems), the protoplast (the cell without the cell wall) imparts a pressure against the cell wall, and hence makes the structure rigid as a whole, even though its individual parts are flaccid. This pressure is called the turgor pressure. Through its action many herbaceous plants, which may contain 80–95% water, are kept upright. Turgor pressure results from the phenomenon of osmosis through semipermeable membranes (in this case the plasma membrane). Details of this will be explained in Section 2.

In contrast to most herbaceous plants, perennial plants contain cells that give support to the structure of the stems and leaves. These may be in the form of actual supporting tissues—collenchyma (living support tissue) or sclerenchyma (dead support tissue, once fully differentiated)—or in the form of water conducting tissue—xylem—of the vascular bundles.

2. Water Potential: What Does it Contain?

In most fully differentiated plant cells the cytoplasm takes up only 5–10% of the cell volume, while the rest is filled by a huge vacuole. The cytoplasm and vacuole contain large quantities of dissolved ions and organic compounds, which impart to them an osmotic potential or solute potential (ψ_s). The osmotic potential can be calculated from van't Hoff equation $\psi_s = -RTc_s$, where R is the gas constant (8.32 J mol⁻¹K⁻¹), T is the absolute temperature (in degrees Kelvin) and c_s the osmolality of the solute concentration (moles of total dissolved solutes per liter of water, mol L⁻¹). Hence, the osmotic potential of pure water is zero. The more solutes there are in the solution, the more negative the osmotic potential will be.

There are other things that affect the state of water inside the cells: these are the pressure, the gravity, and the presence of large organic molecules (or matrix), which may collect a sheet of water molecules around them. Now, these have been given the

terms ψ_p (p for pressure), ψ_g (g for gravity) and ψ_m (m for matrix). All these potentials added together form the water potential (ψ_w) of the cell, and hence we can write the equation:

$$\psi_w = \psi_s + \psi_p + \psi_g + \psi_m \quad (1)$$

While the osmotic potential is either 0 or a negative figure, the pressure potential can vary between positive (turgid cell) or negative (transpirational “pull” in vessels) values. Gravity would impart a positive value, but under normal conditions, when vertical distances are small, it is negligible. The matrix potential can be a positive or negative value depending on the matrix. Normally, all the polymer surfaces of the plant cells are covered by a layer of water molecules, and hence matrix potential is negligible, except in germinating seeds, which contain large amounts of starch and other dry compounds that draw a lot of water molecules to their hydrophilic surfaces, and hence impart a negative ψ_m to the system. Now, we see that the ψ_w can have either 0, a negative or a positive value, although in normal living cells ψ_w is practically always a negative value. The water potential of a particular cell gives us an idea how water molecules travel in the tissues. If two adjacent cells have different water potentials, this means that water is going to pass from one cell to the other until the pressures are equalized. Water moves from higher water potential to lower (more negative) water potential. The passage of water is allowed through particular pores in the plasma membrane called aquaporins. Until a few years ago their existence was not known, but nowadays there is ample information on their presence in membranes. Earlier it was thought that water molecules could work their way between the membrane lipid molecules, and hence pass the membrane. This was, however, against the basic theory of membrane properties, which states that all ions or molecules that are charged or polar cannot pass the membrane, and only small, uncharged (and hence hydrophobic) atoms or molecules can go through the plasma membrane. It is now known that the aquaporins allow the passage of water through the otherwise impermeable membrane. Water flow is regulated by the expression of aquaporins (i.e., their number per area) and by their regulation through protein phosphorylation.

It is now clear that water travels from cell to cell according to the water potential, but if this leads to the equalization of water potentials, then the flow will stop. This is maintained by active transport of ions from cell to cell to keep the water potentials of each cell at a stable level.

3. Absorption of Soil Water by Plant Roots (and Other Parts)

Now that we know how water flow is regulated in tissues by the water potential, it is easy to imagine how the roots take up water. Under normal field conditions the osmotic potential of soil water is about -4 bars and that of the roots about -6 bars, and hence water travels into the roots drawn by the water potential. If the roots are growing in a soil troubled with too much salt, the osmotic potential can be too low; for example, the osmotic potential of 0.5% NaCl-solution is -4.8 bars, 1% -8.3 bars, and 3% -20 bars. It is clear that ordinary land plants cannot take up water from high salt soils (e.g., ocean shores), but instead lose water from their tissues and suffer from drought.

Plant roots take up water from the soil, but it is not the whole root that acts in this uptake. Once the roots grow older, the surface develops a layer of cork (in most cases), which hinders the passage of water. Hence, it is only the root tip area that is active in water absorption. This is why it is so important that plant roots grow constantly. Since the surface area of the root tips is not very great, roots have developed special anatomical features during evolution to enhance their water uptake. In Figure 1, showing a barley root tip (*Hordeum vulgare* cv. Hankkija-673), the surface area is greatly increased by a large amount of root hairs, which are basically outgrowths of single root epidermis or rhizodermis cells. The number of these extensions is huge and it is easy to imagine how they grow between soil particles and in doing so, increase the absorbing surface area of the roots greatly.

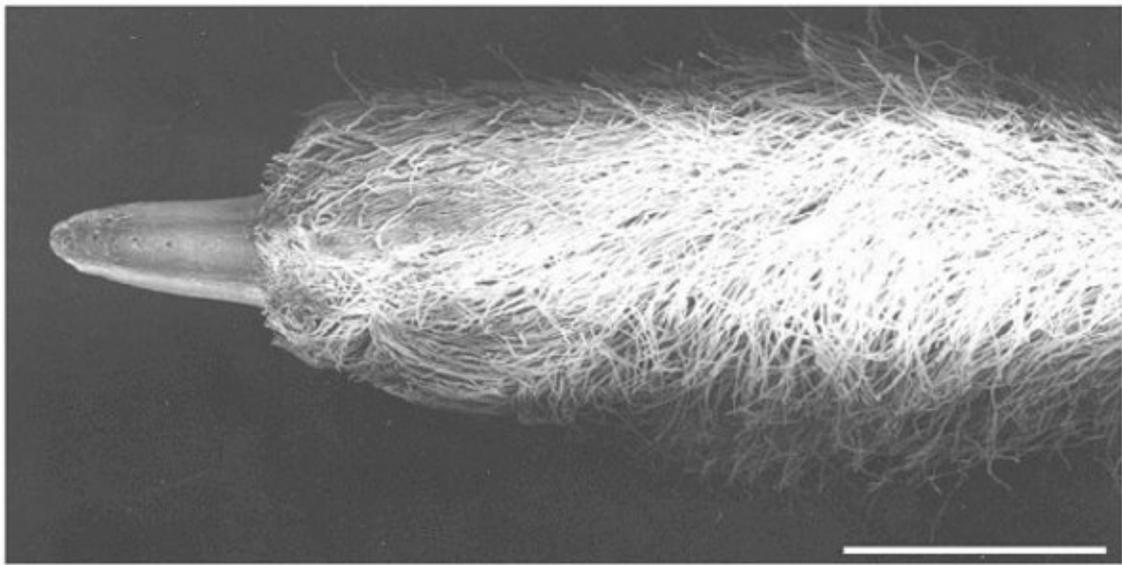


Figure 1. Root tip of a barley plant (*Hordeum vulgare* cv. Hankkija-673) grown in an aerated solution culture

Source: Photograph by Kurt Fagerstedt.

Plant roots are not the only plant organs that can absorb water. If the air contains lots of moisture (fog), plant leaves can absorb this through their epidermis or through stomata. (It has been noticed also that during very heavy and long rainy periods, leaves can lose some of their solutes into the rainwater, and hence suffer from nutrient deficiencies.)

When water is taken up by the roots it does not all enter the cells immediately. In plants, the available space is divided between the symplast (i.e., all the protoplasts—the cells surrounded by the plasma membrane) connected together by plasmodesmata, and the rest of the space, called the apoplast, which covers the cell walls and the intercellular spaces. Water can relatively freely enter the apoplastic space guided by the laws of diffusion and enter the cells of the rhizodermis or any of the cells in the root cortex. Apoplastic diffusion is hindered at the interface between the root cortex and the vascular cylinder by a hydrophobic layer—called Casparian strip—in the cell walls of the endodermis. This means that any water molecules entering the xylem in the vascular cylinder, is going to pass through a layer of live cells, which can effectively regulate water transport.

4. What Else is There in Soil Moisture?

Naturally, it is not only water in the soil that is of significance to plant life; nutrients are of vital importance, too. Soil consists of particles that contain masses of elements in solid form, and these are not available to plants unless they are dissolved in the soil solution. Chemical and physical erosion releases elements from the soil particles, so making them available to plants.

Also, soil particles, which normally have a negative electric charge, bind positively charged soil ions to their surface. Plant roots have developed an ingenious strategy to release these adsorbed ions. Roots extrude protons through specific proton-ATPase complexes on the plasma membrane. These released protons are exchanged to the nutrient ions bound on the soil particles, since protons have a higher affinity to the soil particles than other ions.

It is often thought that plants take up nutrients from the soil with the flow of water from the soil to the roots. This is not so. Charged nutrient ions cannot pass the plant plasma membrane; they have to be taken in through protein pores or channels in the membrane.

If they are taken in against a concentration gradient, the transport consumes energy, which is available in the form of the proton gradient formed by the proton ATPase pump or by direct involvement of ATP in the transport process. The channels of the plasma membrane and the vacuolar tonoplast are collected in Table 1.

PLASMA MEMBRANE (outside pH c. 5.5, cytoplasmic pH c. 7.2, plasma membrane potential-120 mV)	TONOPLAST (vacuolar pH c. 5.5, tonoplast membrane potential -90 mV)
PO ₄ ³⁻ H ⁺ symporter	H ⁺ ATPase pump
NO ₃ ⁻ H ⁺ symporter	H ⁺ PP ₁ pump
K ⁺ H ⁺ Na ⁺ symporter	Na ⁺ H ⁺ antiporter
Sucrose H ⁺ symporter	Ca ²⁺ 3H ⁺ antiporter
Amino acid H ⁺ symporter	Cd ²⁺ H ⁺ antiporter
Na ⁺ H ⁺ antiporter	Mg ²⁺ H ⁺ antiporter
H ⁺ ATPase pump	Hexose sugar H ⁺ antiporter
Sucrose efflux carrier	Sucrose H ⁺ antiporter
Ca ²⁺ ATPase pump	PC-Cd ²⁺ ATPase ABC transporter
Inward rectifying K ⁺ pump	Anthocyanin-GS ATPase ABC transporter
Outward rectifying K ⁺ pump	Anion-cation Slow Vacuolar channel (SV)
Inward rectifying Cl ⁻ pump	Ca ²⁺ IP channel
Outward rectifying Cl ⁻ pump	Anions, malate ²⁻ , Cl ⁻ , NO ₃ ⁻ Fast Vacuolar channel (FV)
Inward rectifying Ca ²⁺ pump	Aquaporin
Aquaporin	

Table 1. Channels of the plant plasma membrane and the vacuolar tonoplast membrane
Note: For details see Taiz and Zeiger.

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Biographical Sketch

Kurt Fagerstedt started his studies in biology at Helsinki University, where he received his M.Sc. degree, majoring in Plant Physiology in 1984. He continued his studies at the University of St Andrews in Scotland, UK, and finished his Ph.D. degree in 1988. He is now a Docent and Senior Lecturer and Vice-head of the Department of Biosciences at Viikki Biocenter of University of Helsinki, Finland. He is currently teaching plant physiology and anatomy, as well as plant ecophysiology and plant biochemistry.

He is a member of the Center of Excellence on Plant Molecular Biology and Tree Biotechnology (granted by the Academy of Finland) and leads a research group working on two topics: (1) Flooding tolerance mechanisms in wild and cultivated plant species, and (2) Lignin biosynthesis in Scots pine, Norway spruce, and silver birch. Methods used in these studies include study of enzyme proteins and their corresponding genes by various types of electrophoresis, PCR, light and electron microscopy (SEM and TEM), protein purification, determination of various enzyme activities, and amounts of metabolites (such as ethanol, carbohydrates, antioxidants, polyphenols, ATP, etc.) by spectrophotometry and nuclear magnetic resonance spectrometry (NMR). He has published 16 scientific articles in refereed international journals and several popular articles and a monograph on the wood structure of Finnish forest tree species. Kurt Fagerstedt is a bachelor and enjoys his gardening hobby in the suburb of Espoo near Helsinki.