Water potential

Water potential is the potential energy of water per unit volume relative to pure water in reference conditions. Water potential quantifies the tendency of water to move from one area to another due to osmosis, gravity, mechanical pressure, or matrix effects such as capillary action (which is caused by surface tension). The concept of water potential has proved useful in understanding and computing water movement within plants, animals, and soil. Water potential is typically expressed in potential energy per unit volume and very often is represented by the .Greek letter ψ

Water potential integrates a variety of different potential drivers of water movement, which may operate in the same or different directions. Within complex biological systems, many potential factors may be operating simultaneously. For example, the addition of solutes lowers the potential (negative vector), while an increase in pressure increases the potential (positive vector). If flow is not restricted, water will move from an area of higher water potential to an area that is lower potential. A common example is water with a dissolved salt, such as sea water or the fluid in a living cell. These solutions have negative water potential, relative to the pure water reference. With no restriction on flow, water will move from the locus of greater potential (pure water) to the locus of lesser (the solution); flow proceeds until the difference in potential is equalized or balanced by another water potential factor, .such as pressure or elevation

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Components of water potential

Many different factors may affect the total water potential, and the sum of these potentials determines the overall water potential and the :direction of water flow

Ψ = Ψ 0 + Ψ π + Ψ p + Ψ s + Ψ v + Ψ m \Psi =\Psi _{0}+\Psi _{\pi }+\Psi _{p}+\Psi _{s}+\Psi _{v}+\Psi _{m}[1

:where

،Ψ 0 \Psi _{0} is the reference correction

،Ψ π \Psi _{\pi } is the solute or osmotic potential

،Ψ p \Psi _{p} is the pressure component

،Ψ s \Psi _{s} is the gravimetric component

Ψ v \Psi _{v} is the potential due to humidity, and

Ψ m \Psi_m is the potential due to matrix effects (e.g., fluid cohesion (.and surface tension

All of these factors are quantified as potential energies per unit volume, and different subsets of these terms may be used for particular applications (e.g., plants or soils). Different conditions are also defined as reference depending on the application: for example, in soils, the reference .condition is typically defined as pure water at the soil surface

Pressure potential

Pressure potential is based on mechanical pressure, and is an important component of the total water potential within plant cells. Pressure potential increases as water enters a cell. As water passes through the cell wall and cell membrane, it increases the total amount of water present inside the cell, which exerts an outward pressure that is opposed by the structural rigidity of the cell wall. By creating this pressure, the plant can maintain turgor, which allows the plant to keep .its rigidity. Without turgor, plants will lose structure and wilt

The pressure potential in a plant cell is usually positive. In plasmolysed cells, pressure potential is almost zero. Negative pressure potentials occur when water is pulled through an open system such as a plant xylem vessel. Withstanding negative pressure potentials (frequently called tension) is an important adaptation of xylem. This tension can be .measured empirically using the Pressure bomb

(Osmotic potential (solute potential

Pure water is usually defined as having an osmotic potential (Ψ π \Psi _{\pi }) of zero, and in this case, solute potential can never be positive.

The relationship of solute concentration (in molarity) to solute potential :is given by the van 't Hoff equation

$\Psi \pi = - M i R T$ \Psi _{\pi }=-MiRT

where M M is the concentration in molarity of the solute, i i is the van 't Hoff factor, the ratio of amount of particles in solution to amount of formula units dissolved, R R is the ideal gas constant, and T T is the .absolute temperature

For example, when a solute is dissolved in water, water molecules are less likely to diffuse away via osmosis than when there is no solute. A solution will have a lower and hence more negative water potential than that of pure water. Furthermore, the more solute molecules present, the .more negative the solute potential is

Osmotic potential has important implications for many living organisms. If a living cell is surrounded by a more concentrated solution, the cell will tend to lose water to the more negative water potential (Ψw \Psi _{w}) of the surrounding environment. This can be the case for marine organisms living in sea water and halophytic plants growing in saline environments. In the case of a plant cell, the flow of water out of the cell may eventually cause the plasma membrane to pull away from the cell wall, leading to plasmolysis. Most plants, however, have the ability to increase solute inside the cell to drive the flow of water into the cell and .maintain turgor

[This effect can be used to power an osmotic power plant.[2

A soil solution also experiences osmotic potential. The osmotic potential is made possible due to the presence of both inorganic and organic solutes in the soil solution. As water molecules increasingly clump around solute ions or molecules, the freedom of movement, and thus the potential energy, of the water is lowered. As the concentration of solutes is increased, the osmotic potential of the soil solution is reduced. Since water has a tendency to move toward lower energy levels, water will want to travel toward the zone of higher solute concentrations. Although, liquid water will only move in response to such differences in osmotic potential if a semipermeable membrane exists between the zones of high and low osmotic potential. A semipermeable membrane is necessary because it allows water through its membrane while preventing solutes from moving through its membrane. If no membrane is present, movement of the solute, rather than of the water, largely .equalizes concentrations

Since regions of soil are usually not divided by a semipermeable membrane, the osmotic potential typically has a negligible influence on the mass movement of water in soils. On the other hand, osmotic potential has an extreme influence on the rate of water uptake by plants. If soils are high in soluble salts, the osmotic potential is likely to be lower in the soil solution than in the plant root cells. In such cases, the soil solution would severely restrict the rate of water uptake by plants. In salty soils, the osmotic potential of soil water may be so low .(that the cells in young seedlings start to collapse (plasmolyze

(Matrix potential (Matric potential

When water is in contact with solid particles (e.g., clay or sand particles within soil), adhesive intermolecular forces between the water and the solid can be large and important. The forces between the water molecules and the solid particles in combination with attraction among water molecules promote surface tension and the formation of menisci within the solid matrix. Force is then required to break these menisci. The magnitude of matrix potential depends on the distances between solid particles—the width of the menisci (also capillary action and differing Pa at ends of capillary)—and the chemical composition of the .(solid matrix (meniscus, macroscopic motion due to ionic attraction

In many cases, absolute value of matrix potential can be relatively large in comparison to the other components of water potential discussed above. Matrix potential markedly reduces the energy state of water near particle surfaces. Although water movement due to matrix potential may be slow, it is still extremely important in supplying water to plant roots and in engineering applications. The matrix potential is always negative because the water attracted by the soil matrix has an energy state lower than that of pure water. Matrix potential only occurs in unsaturated soil above the water table. If the matrix potential approaches a value of zero, nearly all soil pores are completely filled with water, i.e. fully saturated and at maximum retentive capacity. The matrix potential can vary considerably among soils. In the case that water drains into less-moist soil zones of similar porosity, the matrix .potential is generally in the range of −10 to −30 kPa

Empirical examples

Soil-plant-air continuum

Main article: Soil plant atmosphere continuum

At a potential of 0 kPa, soil is in a state of saturation. At saturation, all soil pores are filled with water, and water typically drains from large pores by gravity. At a potential of −33 kPa, or −1/3 bar, (−10 kPa for sand), soil is at field capacity. Typically, at field capacity, air is in the macropores and water in micropores. Field capacity is viewed as the optimal condition for plant growth and microbial activity. At a potential of −1500 kPa, soil is at its permanent wilting point, meaning that soil water is held by solid particles as a "water film" that is retained too .tightly to be taken up by plants

In contrast, atmospheric water potentials are much more negative—a typical value for dry air is −100 MPa, though this value depends on the temperature and the humidity. Root water potential must be more negative than the soil, and the stem water potential and intermediate lower value than the roots but higher than the leaf water potential, to create a passive flow of water from the soil to the roots, up the stem, to [the leaves and then into the atmosphere.[3][4][5

Measurement techniques

A tensiometer, electrical resistance gypsum block, neutron probes, or time-domain reflectometry (TDR) can be used to determine soil water potential energy. Tensiometers are limited to 0 to −85 kPa, electrical resistance blocks is limited to −90 to −1500 kPa, neutron probes is limited to 0 to −1500 kPa, and TDR is limited to 0 to −10,000 kPa. A scale can be used to estimate water weight (percentage composition) if .special equipment is not on hand

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Water absoraption

The absorption of water by plants is essential for various metabolic activities. Land plants get their water supply from soil which serves as the source of water and [minerals]. The way in which water from soil enters roots, particularly to the root xylem, is called "mechanism of water absorption". Both active and passive absorption have been .proposed for mechanism of water absorption

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Active absorption

Active absorption refers to the absorption of water by roots with the help of ATP, generated by the root respiration: as the root cells actively take part in the process, it is called active absorption. According to Renner, active absorption takes place in low transpiring and well-watered plants, and 4% of total water absorption is carried out in this process. The active absorption is carried out by two theories; active osmotic water absorption and Active non-osmotic water absorption. In .this process energy is required

Active osmotic water absorption

This theory was given by Pari (1910) and Priestley (1921). According to this theory, the root cells behave as an ideal osmotic pressure system through which water moves up from the soil solution to the root xylem along an increasing gradient of D.P.D. (suction pressure, which is the real force for water absorption). If solute concentration is high and water potential is low in the root cells, water can enter from soil to root cells through endosmosis. Mineral nutrients are absorbed actively by the root cells due to utilisation of adenosine triphosphate (ATP). As a result, the concentration of ions (osmotica) in the xylem vessels is more in comparison to the soil water. A concentration gradient is established between the root and the soil water. Hence, the solute potential of xylem water is more in comparison to that of soil and correspondingly water potential is low than the soil water.If stated, water potential is comparatively positive in the soil water. This gradient of water potential causes endosmosis. The endosmosis of water continues till the water potential both in the root and soil becomes equal. It is the absorption of minerals that utilise metabolic energy, but not water absorption. Hence, absorption of water is indirectly an active process in a plant's life.Active transport is in an .opposite direction to that of diffusion

Active non-osmotic water absorption

This theory was given by Thimann (1951) and Kramer (1959). According to the theory, sometimes water is absorbed against a concentration gradient. This requires expenditure of metabolic energy released from respiration of root cells. There is no direct evidence, but some scientists suggest involvement of energy from respiration. In conclusion, it is said that, the evidences supporting active absorption .of water are themselves poor

Passive absorption

This mechanism is carried out without utilisation of metabolic energy. Here, only the roots act as an organ of absorption or passage. Hence, sometimes it is called water absorption 'through roots', rather 'by' roots. It occurs in rapidly transpiring plants during daytime, because of opening of stomata and the atmospheric conditions. The force for absorption of water is created at the leaf end i.e. the transpiration pull. The main cause behind this transpiration pull, water is lifted up in the plant axis like a bucket of water is lifted by a person from a well. Transpiration pull is responsible for dragging water at the leaf end, the pull or force is transmitted down to the root through water column in the xylem elements. The continuity of water column remains intact due to the cohesion between the molecules and it act as a rope. Roots simply act as a passive organ of absorption. As transpiration proceeds, simultaneously water absorption also takes place to compensate the water loss from leaf end. Most volume of water entering plants is by means of passive absorption. Passive transport is nothing different from diffusion but just explaining its meaning "passive" refers to requiring no input of energy. There is a free movement of molecules from their higher concentration to their lower concentration. The water will enter the plant via the root cells that can be found in the roots where mainly passive absorption occurs. Also, with the absorption of water, minerals and nutrients are als

Mechanism of Absorption of Water

In higher plants water is absorbed through root hairs which are in contact with soil water and form a root hair zone a little behind the root tips (Fig. 4.1). Root hairs are tubular hair like prolongations of the cells of the epidermal layer (when epidermis bears root hairs it is also known as piliferous layer) of the roots. The walls of root hairs are permeable and consist of pectic substances and cellulose which are strongly hydrophilic (water loving) in nature. Root hairs contain .vacuoles filled with cell sap

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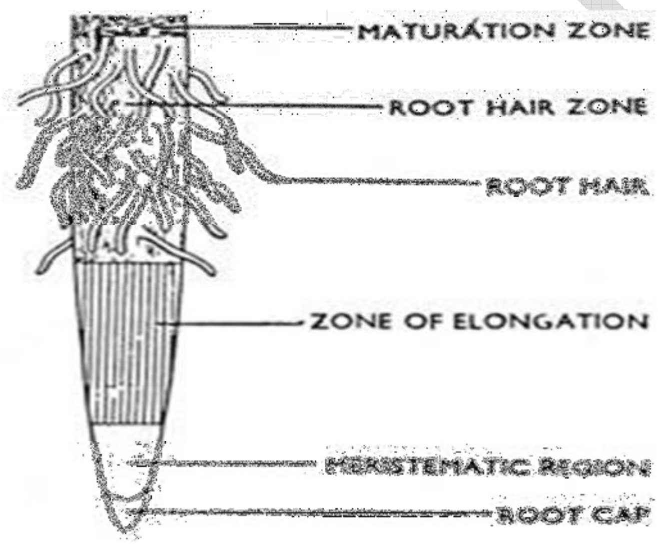

Fig. 4.1. Diagrammatic representation of a root tip showing root hair zone.

(1) Active Absorption of Water:

In this process the root cells play active role in the absorption of water and metabolic energy released through respiration is consumed.

ADVERTISEMENTS:

Active absorption may be of two kinds:

(a) Osmotic absorption i.e., when water is absorbed from the soil into the xylem of the roots according to the osmotic gradient.

(b) Non-osmotic absorption i.e., when water is absorbed against the osmotic gradient.

(2) Passive Absorption of Water:

It is mainly due to transpiration, the root cells do not play active role and remain passive.

(1a) Active Osmotic Absorption of Water:

First step in the osmotic absorption of water is the imbibition of soil water by the hydrophilic cell walls of root hairs. Osmotic Pressure (O.P.) of the cell-sap of root hairs is usually higher than the O.P. of the soil water. Therefore, the Diffusion Pressure Deficit (D.P.D.) and the suction pressure in the root hairs become higher and water from the cell walls enters into them through plasma-membrane (semi-permeable) by osmotic diffusion. As a result, the O.P., suction pressure and D.P.D. of root hairs now become lower, while their turgor pressure is increased.

Now, the cortical cells adjacent to root hairs have higher O.P., suction pressure and D.P.D. in comparison to the root hairs. Therefore, water is drawn into the adjacent cortical cells from the root-hairs by osmotic diffusion.

In the same way, the water by cell to cell osmotic diffusion gradually reaches the innermost cortical cells and the endodermis. Osmotic diffusion of water into endodermis takes place through special thin walled passage cells because the other endodermal cells have casparian strips on their walls which are impervious to water (Fig. 4.2).

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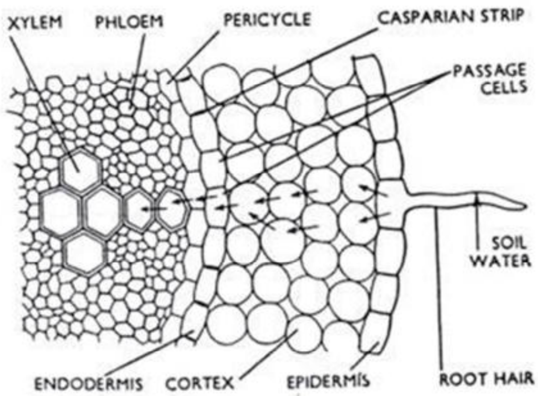

Fig. 4.2. A part of T.S. of typical dicot root. The arrows indicate the path of water.

Water from endodermal cells is drawn into the cells of pericycle by osmotic diffusion which now becomes turgid and their suction pressure is decreased. In the last step, water is drawn into xylem from turgid pericycle cells. (In roots the vascular bundles are radial and protoxylem elements are in contact with pericycle).

It is because in absence of turgor pressure of the xylem vessels (which are non-elastic), the suction pressure of xylem vessels becomes higher than the suction pressure of the cells of the pericycle. When water enters into xylem from pericycle, a pressure is developed in the xylem of roots which can raise the water to a certain height in the xylem. This pressure is called as root pressure.

(1b) Active Non-Osmotic Absorption of Water:

Sometimes, it has been observed that absorption of water takes place even when the O.P. of the soil water is higher than the O.P. of cell-sap. This type of absorption which is non- osmotic and against the osmotic gradient requires the expenditure of metabolic energy probably through respiration.

Following evidences support this view:

(i) The factors which inhibit respiration also decrease water absorption.

(ii) Poisons which retard metabolic activities of the root cells also retard water absorption.

(iii) Auxins (growth hormones) which increase metabolic activities of the cells stimulate absorption of water.

(2) Passive Absorption of Water:

Passive absorption of water takes place when rate of transpiration is usually high. Rapid evaporation of water from the leaves during transpiration creates a tension in water in the xylem of the leaves. This tension is transmitted to water in xylem of roots through the xylem of stem and the water rises upward to reach the transpiring surfaces.

As a result, soil water enters into the cortical cells through root hairs to reach the xylem of roots to maintain the supply of water. The force for this entry of water is created in leaves due to rapid transpiration and hence, the root cells remain passive during this process.

During absorption of water by roots, the flow of water from epidermis to endodermis may take place through three different pathways:

(i) Apoplastic pathway (cell walls and intercellular spaces),

(ii) Trans-membrane pathway (by crossing the plasma membranes) and

(iii) Symplast pathway (through plasmodesmata).

The mechanism of water absorption described earlier, in-fact belongs to the second category. The relative importance of these three pathways in water absorption by roots is not clearly established. However, a combination of these three pathways is responsible for transport of water across the root.

External Factors Affecting Absorption of Water:

1. Available Soil Water:

Sufficient amount of water should be present in the soil in such form which can easily be absorbed by the plants. Usually the plants absorb capillary water i.e., water present in films in between soil particles. Other forms of water in the soil e.g., hygroscopic water, combined-water, gravitational water etc. are not easily available to plants. Increased amount of water in the soil beyond a certain limit results in poor aeration of the soil which retards metabolic activities of root cells like respiration and hence, the rate of water absorption is also retarded.

2. Concentration of the Soil Solution:

Increased conc. of soil solution (due to the presence of more salts in the soil) results in higher osmotic pressure. If the O.P. of soil solution will become higher than the O.P. of cell sap in root cells, the water absorption particularly the osmotic absorption of water will be greatly suppressed. Therefore, absorption of water is poor in alkaline soils and marshes.

3. Soil Air:

Absorption of water is retarded in poorly aerated soils because in such soils deficiency of O_1 and consequently the accumulation of CO_2 will retard the metabolic activities of the roots like respiration. This also inhibits rapid growth and elongation of the roots so that they are deprived of the fresh supply of water in the soil. Water logged soils are poorly aerated and hence, are physiologically dry. They are not good for absorption of water.

4. Soil Temperature:

Increase in soil temperature up to about 30°C favours water absorption. At higher temperatures water absorption is decreased. At low temp, also water absorption decreases so much so that at about 0°C it is almost checked.

This is probably because at low temp:

(i) The viscosity of water and protoplasm is increased,

(ii) Permeability of cell membranes is decreased,

(iii) Metabolic activities of root cells are decreased, and

(iv) Growth and elongation of roots are checked.

Relative Importance of Active and Passive Absorption of Water:

There are two views regarding the relative importance of active and passive absorption of water in the water economy of plants. Many workers in the past regarded the active absorption of water to be the main mechanism of water absorption and gave very little importance to the passive absorption. But according to Kramer (1969) the active absorption of water is of negligible importance in the water economy of most or perhaps all plants.

He regards the root pressure and the related phenomena involved in the active absorption of water as mere consequences of salt accumulation in the xylem of different kinds of roots. The salt accumulation produces a difference in water potential which brings about the inward movement of water (osmotic uptake) and development of a pressure in the xylem sap (root pressure).

There are many reasons for regarding the active absorption as unimportant:

(i) The volume of exudates from the cut stump is very small in comparison to the volume of water lost in transpiration by the similar intact plants under conditions favourable for transpiration.

(ii) Intact transpiring plants can absorb water from more concentrated and drier soil solutions more easily than the similar de-topped plants.

(iii) No root pressure can be demonstrated in rapidly transpiring plants. Such plants may show even a negative root pressure (i.e., if a little water is placed over the cut stump it is absorbed by the latter).

(iv) In conifers root pressure has rarely been observed.

It is held by certain workers that though the active absorption is not important quantitatively, it occurs all the time and supplements passive absorption. Two main arguments are against this view. Firstly, during periods of rapid transpiration the salts are removed from the root xylem so that their concentration becomes very low.

Under such conditions the osmotic uptake of water cannot be expected to occur. Secondly, even if we suppose that the salts are not removed during periods of rapid transpiration, the latter reduces the water potential of the cortical cells in roots to such a low level that the osmotic entry of water from cortex to xylem is not possible.

The available evidence suggests that usually the water is pulled passively into the plant through the roots by forces which are developed in the transpiring surfaces of the shoot. But under certain conditions such as warm moist soil and low rate of transpiration, salts accumulate in xylem of roots resulting in active osmotic absorption of water.

Field Capacity or Water Holding Capacity of the Soil:

After heavy rainfall or irrigation of the soil, some water is drained off along the slopes while the rest percolates down in the soil. Out of this latter water some amount of water gradually reaches the water table under the force of gravity (gravitational water) while the rest is retained by the soil. This amount of water retained by the soil after the drainage of gravitational water has become very slow is called as field capacity or the water holding capacity of the soil.

The field capacity is affected by soil profile, soil structure and temperature. For instance a fine textured soil overlying a coarse textured soil will have a higher field capacity than a uniformly fine textured soil. Similarly, the field capacity increases with decreasing temperature and vice versa.

Permanent Wilting Percentage or Wilting Coefficient:

The percentage of the soil water left after the plant growing in that soil has permanently wilted is called as permanent wilting percentage or the wilting coefficient. The permanent wilting percentage can be determined by growing the seedlings in small containers under conditions of adequate water supply till they develop several leaves. The soil surface is then covered and the water supply is cut until wilting occurs. The containers are now transferred to humid chamber.

If the plants do not recover, they are considered to be permanently wilted. Otherwise, they are again transferred to normal atmospheric conditions. This process is repeated till they are permanently wilted. The percentage of the soil water is determined at this point after removing the plants from the containers and shaking off as much soil from their roots as possible.

Earlier workers thought permanent wilting percentage to be a soil moisture constant. This view has been strongly criticised by Slatyer (1957) who pointed out that permanent wilting percentage of a soil is dependent on the osmotic characteristics of the plant and is not a soil-moisture constant. Thus the different plants if grown in the same soil wilt at different times depending upon their osmotic potential after the water supply to the soil is stopped.

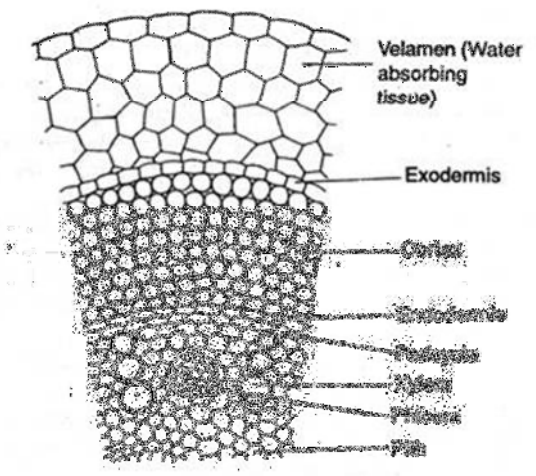

Fig. 4.3 T.S. of a part of aerial root of an orchid showing velamen.

Aquaporins:

In recent years some integral membrane proteins have been discovered which form water selective channels in cell membranes (lipid bilayers) and facilitate faster movement of water across the membranes into the plant cells. These channels have been called as aquaporins (Fig. 4.4). The direction of water transport across the membranes however, is not affected by aquaporins.

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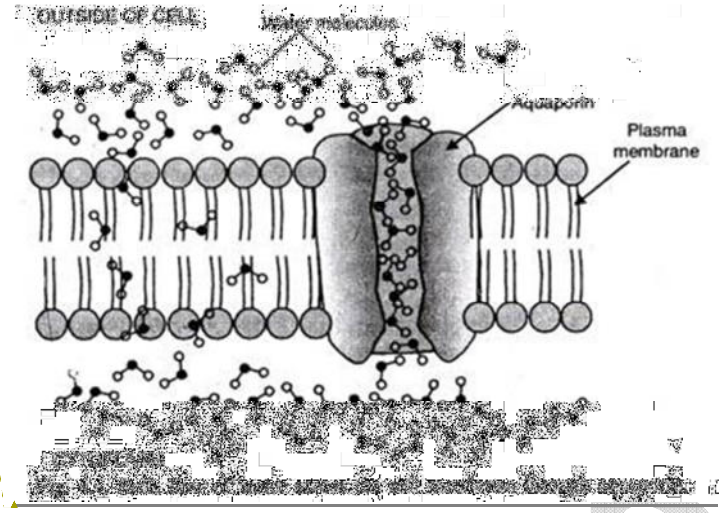

Aquaporin’s are found in both plant and animal membranes but they are relatively abundant in plants. The aquaporin’s satisfactorily account for the observed rate of water movement across the membranes which could not be explained earlier simply by direct diffusion of water through lipid bilayer as the latter does not allow bulk flow of water across it.

According to Tyerman et al (2002), expression and activity of aquaporin’s appear to be regulated probably by protein phosphorylation in response to availability of water.

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