

THE MECHANISMS, THEORY, ABSORPTION, AND TRANSPORTATION OF NUTRIENTS IN PLANTS.

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Abstract

Nutrient acquisition and translocation in plants are fundamental processes that sustain growth, development, and productivity. Nutrient movement begins in the soil through mass flow, diffusion, and root interception, followed by uptake into root cells via apoplastic and symplastic pathways. Plants need various essential nutrients to survive and to develop adequately. These nutrients are needed in sufficient amounts and accessible for plant uptake. Furthermore, nutritional necessities change from one plant species to another and from one plant growth stage to another. Roots transport nutrients further into the plant. It is not uncommon for plant roots to develop in soils with under 3% of accessible nutrients. They need more nutrients, including calcium and magnesium, for their normal life cycle, yet these soils require modest quantities of other nutrients, such as potassium and phosphorus. The accessibility of nutrients facilitates their transfer from soil to the plant roots through an assortment of mechanisms. While the nutrient transit depends on mass flow, diffusion, and root interception. The paper aims to explore the current state of the art in the world of nutrient transport systems for plant survival. The structures involved, the mechanism of absorption, and ion exchange mechanisms are discussed. Factors affecting plant nutrient uptake, in relation to the percentage of nutrients in the soil solution, and some characteristics of the ion transport mechanisms that directly influence soil-based nutrient uptake processes are also highlighted.

Keywords: Nutrient, Ion uptake kinetics, Ion absorption measurement, Ion translocation.

1. Introduction:

Plant nutrition is a fundamental aspect of plant biology, governing how plants obtain and utilize essential mineral elements required for growth and metabolic functioning. Unlike animals, plants synthesize their own food through photosynthesis, yet they still depend on external sources for minerals that support biochemical and physiological processes. These nutrients are absorbed largely from the soil solution through roots and subsequently distributed throughout the plant.

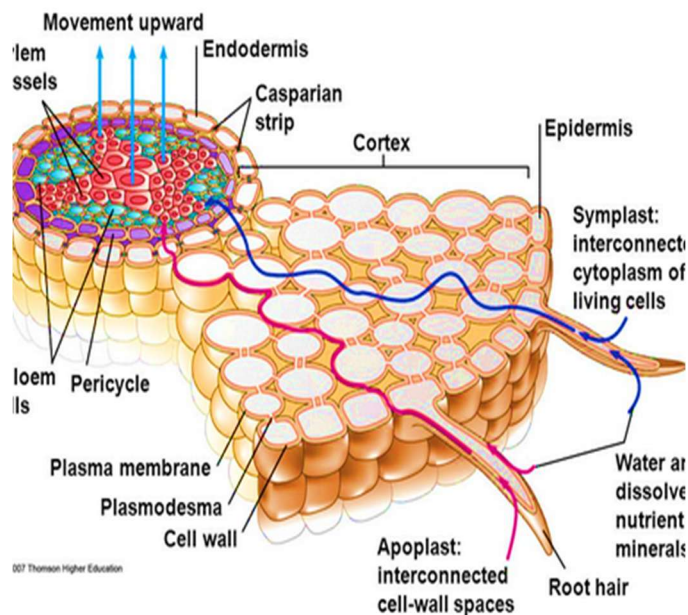


Figure 1: Symplast and Apoplast Pathways in Plants

The availability, mobility, and balance of nutrients determine plant health and productivity. Essential nutrients are categorized into macronutrients and micronutrients based on plant requirements. Macronutrients such as nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur are required in relatively large quantities (Khoso et al., 2024). They form key structural and functional components of plant tissues, including proteins, nucleic acids, membranes, and chlorophyll. Micronutrients such as iron, zinc, manganese, copper, boron, molybdenum, and chlorine, though needed in smaller amounts, are indispensable for enzyme activation and regulatory functions.

Nutrient availability in soil is strongly influenced by physical, chemical, and biological factors. Soil pH affects the solubility of many nutrients, with acidic conditions often limiting phosphorus and molybdenum availability while enhancing iron and manganese solubility. Soil texture determines the capacity to retain nutrients; for instance, clay soils can hold more nutrients than sandy soils. Organic matter contributes to nutrient retention, microbial activity, and improved soil

structure (Bruyant et al., 2024). Root systems play a central role in nutrient acquisition. Their architecture—including length, density, branching patterns, and surface area—determines how effectively they explore the soil environment. Fine root hairs increase absorptive capacity and enable plants to access nutrients that are immobile in soil, such as phosphorus (Barker & Pilbeam, 2015). Root growth patterns also respond dynamically to nutrient patches, enhancing uptake efficiency in heterogeneous soils. Plants employ sophisticated uptake mechanisms involving specific transport proteins embedded in root cell membranes. These transporters regulate the entry of nutrients such as nitrate, phosphate, potassium, and various metal ions. The uptake process is selective and tightly controlled to maintain nutrient homeostasis and prevent toxicity (Koch & Sessitsch, 2024). Once inside the plant, nutrients are transported through xylem and phloem to reach growing tissues, storage organs, and metabolic sites. Nutrient deficiencies lead to characteristic symptoms that reflect the physiological roles of specific elements. Chlorosis, necrosis, stunted growth, and poor root development often indicate imbalances in nutrient supply. Understanding these symptoms helps diagnose nutritional disorders and guide soil amendment strategies. In agriculture, maintaining an optimal nutrient balance is crucial not only for yield but also for produce quality. Environmental stresses such as drought, salinity, and temperature extremes affect nutrient uptake by altering root function, soil chemistry, and microbial communities. Under such stresses, plants may adjust their nutrient requirements or modify transport processes to maintain internal balance. Nutrient-efficient cultivars capable of sustaining growth in challenging environments are increasingly important in modern crop improvement efforts. Advances in plant genomics and molecular biology have expanded our understanding of nutrient signaling pathways. Genes encoding nutrient transporters, transcription factors, and regulatory proteins are now being explored as targets for genetic engineering and breeding programs. These advances support the development of crops with improved nutrient use efficiency, contributing to sustainable agricultural practices and reduced fertilizer dependency. Souri & Hatamian (2019)

2. Essentiality of Elements in Plant Nutrition

A mineral element is considered essential to plant growth and development if the element is involved in plant metabolic functions and the plant cannot complete its life cycle without the element. Usually the plant exhibits a visual symptom indicating a deficiency in a specific nutrient, which normally can be corrected or prevented by supplying the nutrient. Terms commonly used to describe levels of nutrients in plants:

2.1. Deficient: When the concentration of an essential element is low enough to limit yield severely and distinct deficiency symptoms are visible. Extreme deficiencies can result in plant

death. With moderate or slight deficiencies, symptoms may not be visible, but yields will still be reduced.

2.2. Critical range: The nutrient concentration in the plant below which a yield response to added nutrient occurs. Critical levels or ranges vary among plants and nutrients but occur somewhere in the transition between nutrient deficiency and sufficiency.

2.3. Sufficient: The nutrient concentration range in which added nutrient will not increase yield but can increase nutrient concentration. The term *luxury consumption* is often used to describe nutrient absorption by the plant that does not influence yield.

2.4. Excessive or toxic: When the concentration of essential or other elements is high enough to reduce plant growth and yield. Excessive nutrient concentration can cause an imbalance in other essential nutrients, which also can reduce yield.

3. Essential Elements

Sixteen elements are considered essential to plant growth. Carbon (C), hydrogen (H) and oxygen (O) are the most abundant elements in plants. The photosynthetic process in green leaves converts CO₂ and H₂O into simple carbohydrates from which amino acids, sugars, proteins, nucleic acid and other organic compounds are synthesized. Carbon, H and O are not considered mineral nutrients. The supply of CO₂ is relatively constant. The supply of H₂O rarely limits photosynthesis directly but does indirectly through the various effects resulting from moisture stress.

The remaining 13 essential elements are classified as macronutrients and micronutrients and the classification is based on their relative abundance in plants. The macronutrients are nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca) and magnesium (Mg). Compared to the macronutrients, the concentrations of the seven micronutrients – iron (Fe), zinc (Zn), manganese (Mn), copper (Cu), boron (B), chlorine (Cl) and molybdenum (Mo) – are very small. Five additional elements – sodium (Na), cobalt (Co), vanadium (Va), nickel (Ni) and silicon (Si) have been established as essential micronutrients in some plants. Micronutrients are often referred to as minor elements, but this does not mean that they are less important than macronutrients. Micronutrient deficiency or toxicity can reduce plant yield similar to macronutrient deficiency or toxicity.

In fact, plants absorb many nonessential elements, and over 60 elements have been identified in plant materials. When plant material is burned, the remaining plant ash contains all the essential and nonessential mineral elements except C, H, O, N and S, which are burnt off as gases.

Soil, climate, crop variety, and management factors exert considerable influence on plant composition. Because many biological and chemical reactions occur with fertilizers in soils, the quantity of nutrients absorbed by plants does not equal the quantity applied as a fertilizer. Proper fertilizer management

can maximize the proportion of fertilizer nutrient absorbed by the plant. As plants absorb nutrients from the soil, complete their life cycle and die, the nutrients in the plant residue are returned to the soil. These plant nutrients are subject to the same biological and chemical reactions as fertilizer nutrients. Although this cycle varies somewhat among nutrients, understanding nutrient dynamics in the soil plant atmosphere system is essential to successful fertilizer management.

Table 1. Essential Nutrients for plant growth and Their Principal Forms for uptake

Nutrient	Chemical Symbol	Principal forms for uptake
Carbon	C	CO ₂
Hydrogen	H	H ₂ O
Oxygen	O	H ₂ O, O ₂
Nitrogen	N	NH ₄ ⁺ , NO ₃ ⁻
Phosphorus	P	H ₂ PO ₄ ⁻ , HPO ₄ ²⁻
Potassium	K	K ⁺
Calcium	Ca	Ca ²⁺
Magnesium	Mg	Mg ²⁺
Sulfur	S	SO ₄ ²⁻ , SO ₂
Iron	Fe	Fe ²⁺ , Fe ³⁺
Manganese	Mn	Mn ²⁺
Boron	B	H ₃ BO ₃
Zinc	Zn	Zn ²⁺
Copper	Cu	Cu ²⁺
Molybdenum	Mo	MoO ₄ ²⁻
Chlorine	Cl	Cl ⁻

Table 2: Relative and Average Plant Nutrient Concentrations:

Plant Nutrient	Average Concentration*
H	6.0%
O	45.0%
C	45.0%
N	1.5%
K	1.0%
Ca	0.5%
Mg	0.2%
P	0.1%
S	0.1%
Cl	100 ppm (0.01%)
Fe	100 ppm
B	20 ppm
Mn	50 ppm
Zn	20 ppm
Cu	6 ppm
Mo	0.1 ppm

Table 3: Functions of Essential Nutrients in Plants

Nutrient	Function
Carbon	Basic molecular component of carbohydrates, proteins, lipids, and nucleic acids.
Oxygen	Oxygen is somewhat like carbon in that it occurs in virtually all organic compounds of living organisms.
Hydrogen	Hydrogen plays a central role in plant metabolism. Important in ionic balance and as main reducing agent and plays a key role in energy relations of cells.
Nitrogen	Nitrogen is a component of many important organic compounds ranging from proteins to nucleic acids.
Phosphorus	Central role in plants is in energy transfer and protein metabolism.
Potassium	Helps in osmotic and ionic regulation. Potassium functions as a cofactor or activator for many enzymes of carbohydrate and protein metabolism.
Calcium	Calcium is involved in cell division and plays a major role in the maintenance of membrane integrity.
Magnesium	Component of chlorophyll and a cofactor for many enzymatic reactions.
Sulfur	Sulfur is somewhat like phosphorus in that it is involved in plant cell energetic.
Iron	An essential component of many heme and nonheme Fe enzymes and carries, including the cytochromes (respiratory electron carriers) and the ferredoxins. The latter are involved in key metabolic function such as N fixation, photosynthesis, and electron transfer.
Zinc	Essential component of several dehydrogenases, and peptidases, including carbonic anhydrase, alcohol dehydrogenase, glutamic dehydrogenase, and malic dehydrogenase, among others.
Manganese	Involved in the O ₂ – evolving system of photosynthesis and is a component of the enzymes arginase and phosphotransferases.
Copper	Constituent of a number of important enzymes, including cytochrome oxidase, ascorbic acid oxidase, and laccase.
Boron	Involved in carbohydrate metabolism and synthesis of cell wall components.
Molybdenum	Required for the normal assimilation of N in plants. An essential component of nitrate

	reductase as well as nitrogenase (N ₂ fixation enzyme)
Chlorine	Essential for photosynthesis and as an activator of enzymes involved in splitting water. It also functions in osmoregulation of plants growing on saline soils.

4. Plant Nutrients and Their Functions

Plants require a varied range of elements to grow, maintain physiological functions, and reproduce. Of these elements, carbon, hydrogen, and oxygen are absorbed from the air and from water. Some others, such as chloride and nickel, are needed in trace amounts that are usually found in soil. All the rest must be added by fertilization.

Plant nutrition is the study of the chemical elements and compounds necessary for plant growth and reproduction, plant metabolism, and their external supply. In its absence the plant is unable to complete a normal life cycle, or the element is part of some essential plant constituent or metabolite. This is in accordance with Justus von Liebig's law of the minimum. The total essential plant nutrients include seventeen different elements: carbon, oxygen, and hydrogen, which are absorbed from the air and water, whereas other nutrients, including nitrogen, are typically obtained from the soil (exceptions include some parasitic plants). Seventeen elements or nutrients are essential for plant growth and reproduction. They are carbon (C), hydrogen (H), oxygen (O), nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), magnesium (Mg), iron (Fe), boron (B), manganese (Mn), copper (Cu), zinc (Zn), molybdenum (Mo), nickel (Ni), and chlorine (Cl). Nutrients required for plants to complete their life cycle are considered essential nutrients. Nutrients that enhance the growth of plants but are not necessary to complete the plant's life cycle are considered non-essential. Except for carbon, hydrogen, and oxygen, which are supplied by carbon dioxide and water, and nitrogen, provided through nitrogen fixation, the nutrients derive originally from the mineral component of the soil. The law of the minimum states that when the available form of a nutrient is not in enough proportion in the soil solution, other nutrients cannot be taken up at an optimum rate by a plant. A particular nutrient ratio (stoichiometry) of the soil solution is thus mandatory for optimizing plant growth, a value that might differ from nutrient ratios calculated from plant composition.

Plant uptake of nutrients can only proceed when present in a plant-available form. In most situations, nutrients are absorbed in an ionic form from (or together with) soil water. Although minerals are the origin of most nutrients, and the bulk of most nutrient elements in the soil is held in crystalline form within primary and secondary minerals, they weather too slowly to support rapid plant growth. For example, the application of finely ground minerals, feldspar and apatite, to

soil seldom provides the necessary amounts of potassium and phosphorus at a rate sufficient for good plant growth, as most of the nutrients remain bound in the crystals of those minerals. However, plants are able to stimulate mineral weathering, and thus the availability of mineral-bound nutrients, through various processes, both direct (e.g. weathering agents such as carbon dioxide, organic acids and ligands) and indirect (e.g. mycorrhizal fungi, rhizosphere bacteria).^{[159][160][161]}

The nutrients adsorbed onto the surfaces of clay colloids and soil organic matter provide a more accessible reservoir of many plant nutrients (e.g., K, Ca, Mg, P, Zn). As plants absorb the nutrients from the soil water, the soluble pool is replenished from the surface-bound pool. Plants must obtain the following mineral nutrients from their growing medium:

4.1. The macronutrients: nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), sulfur (S), magnesium (Mg), carbon (C), hydrogen (H), oxygen (O)

4.2. The micronutrients (or trace

minerals): Iron (Fe), boron (B), chlorine (Cl), manganese (Mn), zinc (Zn), copper (Cu), molybdenum (Mo), and nickel (Ni). These elements stay beneath soil as salts, so plants absorb these elements as ions. The macronutrients are taken up in larger quantities; hydrogen, oxygen, nitrogen, and carbon contribute to over 95% of a plant's entire biomass on a dry matter weight basis. Micronutrients are present in plant tissue in quantities measured in parts per million, ranging from 0.1 to 200 ppm, or less than 0.02% dry weight.

Most soil conditions across the world can provide plants adapted to that climate and soil with sufficient nutrition for a complete life cycle, without the addition of nutrients as fertilizer. However, if the soil is cropped, it is necessary to artificially modify soil fertility through the addition of fertilizer to promote vigorous growth and increase or sustain yield. This is done because, even with adequate water and light, nutrient deficiency can limit growth and crop yield.

Table 4: Form, source, mode of uptake, and major functions of 16 plant essential nutrients

Nutrient Family	Nutrient	Percentage of plant	Form taken up by plant (ion)	Mode of uptake	Major functions in plants
Primary	Carbon	45	Carbon dioxide (CO ₂), bicarbonate (HCO ₃)	Open stomates	Plant structures
Primary	Oxygen	45	Water (H ₂ O)	Mass flow	Respiration, energy production, plant structures

Primary	Hydrogen	6.0	Water (H ₂ O)	Mass flow	pH regulation, water retention, synthesis of carbohydrates
Primary	Nitrogen	1.75	Nitrate (NO ₃), ammonium (NH ₄ ⁺)	Mass flow	Protein/amino acids, chlorophyll, cell formation
Primary	Phosphorous	0.25	Dihydrogen phosphate (H ₂ PO ₄ ⁻ , HPO ₄ ²⁻), phosphate (PO ₄ ³⁻)	Root interception	Cell formation, protein syntheses, fat and carbohydrate metabolism
Primary	Potassium	1.5	Potassium ion (K ⁺)	Mass flow	Water regulation, enzyme activity
Secondary	Calcium	0.50	Calcium ion (Ca ²⁺)	Mass flow	Root permeability, enzyme activity
Secondary	Magnesium	0.20	Magnesium ion (Mg ²⁺)	Mass flow	Chlorophyll, fat formation and metabolism
Secondary	Sulfur	0.03	Sulfate (SO ₄ ²⁻)	Mass flow	Protein, amino acid, vitamin and oil formation
Micro	Chlorine	0.01	Chloride (Cl ⁻)	Root interception	Chlorophyll formation, enzyme activity, cellular development
Micro	Iron	0.01	Iron ion (Fe ²⁺ , Fe ³⁺)	Root interception	Enzyme development and activity
Micro	Zinc	0.002	Zinc ion (Zn ²⁺)	Root interception	Enzyme activity
Micro	Manganese	0.005	Manganese ion (Mn ²⁺)	Root interception	Enzyme activity and pigmentation
Micro	Boron	0.0001	Boric acid (H ₃ BO ₃), borate (BO ₃ ³⁻), and tetraborate (B ₄ O ₇)	Root interception	Enzyme activity

Micro	Copper	0.0001	Copper ion (Cu ²⁺)	Mass flow	Enzyme activity
Micro	Molybdenum	0.00001	Molybdenum ions (MoO ₄ ⁻ , MoO ₄ ²⁻)	Mass flow	Enzyme activity and nitrogen fixation in legumes

4.4. Transportation Plant Nutrients in Plants

Plants transport water, minerals, and nutrients throughout their tissues using two main mechanisms:

4.4.1. Xylem: Xylem vessels are responsible for the upward movement of water and minerals from the roots to the leaves. Water is absorbed by the roots from the soil and then transported upwards through the xylem vessels by a process called transpiration. Transpiration occurs when water evaporates from the leaves and creates a suction that pulls water up through the xylem.

4.4.2. Phloem: Phloem vessels are responsible for the downward movement of sugars and other organic compounds from the leaves to the rest of the plant. Sugars are produced in the leaves through photosynthesis and then transported to other parts of the plant for growth and energy production. The transportation of water, minerals, and nutrients in plants is essential for their survival and growth. Without these mechanisms, plants would not be able to access the resources they need to photosynthesize and produce food. Water absorption in plants is a crucial process that enables them to transport water and nutrients from the soil to various parts of the plant body. It occurs primarily through the roots, which are specially adapted for this purpose. Here's a more in-depth explanation of water absorption in plants:

1. Root Structure:

The roots of plants consist of tiny root hairs, which are hair-like projections that increase the surface area for water absorption. Root hairs are located in the zone of maturation, just behind the root tip. The root cap protects the delicate root meristem and helps the root penetrate the soil.

2. Osmosis and Active Transport:

Water absorption in plants mainly occurs through osmosis, a process by which water molecules move from an area of lower solute concentration to an area of higher solute concentration through a semipermeable membrane.

The root hair cells have a higher concentration of solutes compared to the soil solution, creating a concentration gradient. Water molecules move into the root hair cells by osmosis, causing them to become turgid and expand. Active transport also plays a role in water absorption, particularly in cases where the soil water potential is low. Root cells actively transport ions, such as potassium and nitrate, into the root, creating a more negative water potential inside the root.

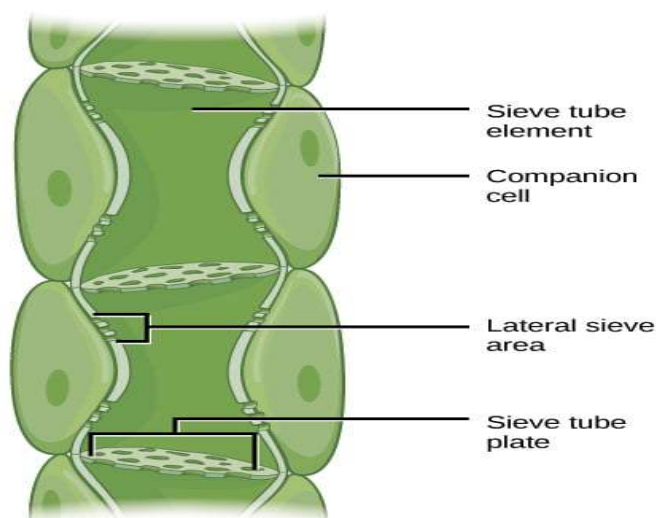


Figure 2: Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells. Image credit: OpenStax Biology. Source: Kerr, S.C., Weigel, E., Spencer, C.C., Garton, D., Richards, R., Birol, O., & L.E. Green. 2025

3. Apoplastic and Symplastic Pathways:

Water absorption in plants is a complex and finely regulated process crucial for their survival and optimal growth. This multifaceted journey of water from the soil to the various plant tissues involves several distinct pathways. Each of these pathways, known as the symplast, apoplast, and transmembrane pathways, plays a significant role in facilitating the movement of water through plant roots and ultimately into the entire plant system.

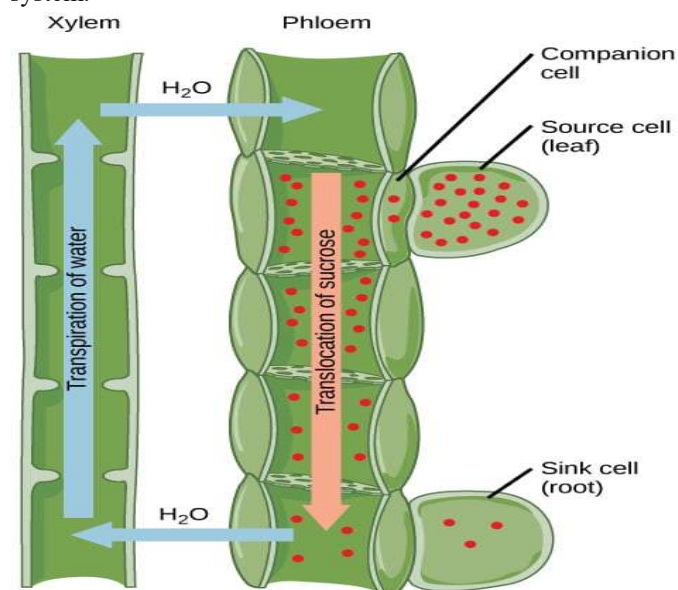


Figure 3: Sucrose is actively transported from source cells

into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels. Image credit: OpenStax Biology. Source: Kerr, S.C., Weigel, E., Spencer, C.C., Garton, D., Richards, R., Birol, O., & L.E. Green. 2025

Water Absorption in Plants

1. Symplast Pathway:

The symplast pathway represents the movement of water through the living components of plant cells. This journey occurs through the interconnected protoplasts, which are the living contents of plant cells, linked by channels called plasmodesmata. Plasmodesmata provide a direct route for water to flow from one cell to another, bypassing the cell walls. This pathway is highly controlled and allows for the transport of water along a continuum of living cells, facilitating efficient and regulated movement throughout the plant.

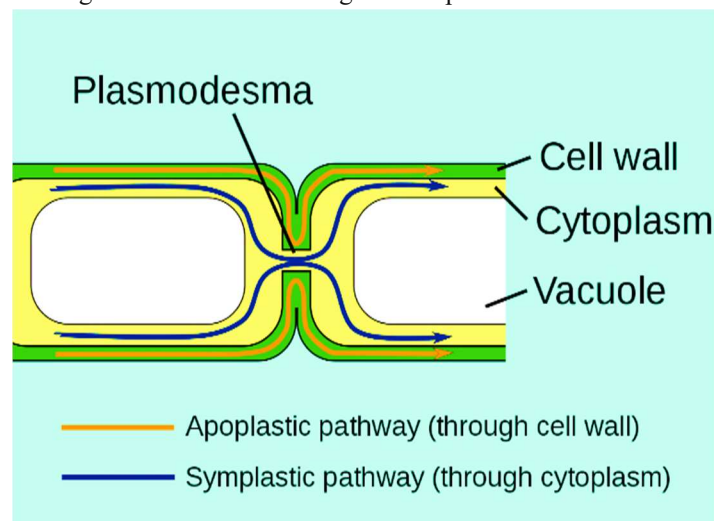


Figure 4: Apoplast and symplast pathway

The Symplastic transport of water involves the cytoplasm, endoplasmic reticulum, and other organelles within plant cells. It is particularly important in the uptake of water from the soil into the root hairs and the subsequent transport through the root cortex. The symplast pathway enables plants to coordinate responses to changing environmental conditions, ensuring adaptability and efficiency in water absorption.

2. Apoplast Pathway:

In contrast, the apoplast pathway involves the non-living components of plant tissues, specifically the cell walls and intercellular spaces. Water can move freely through these extracellular spaces without entering the protoplasts, providing a rapid and less regulated route for water transport. The apoplast pathway is critical for the movement of water within the root cell walls, facilitating quick uptake from the soil.

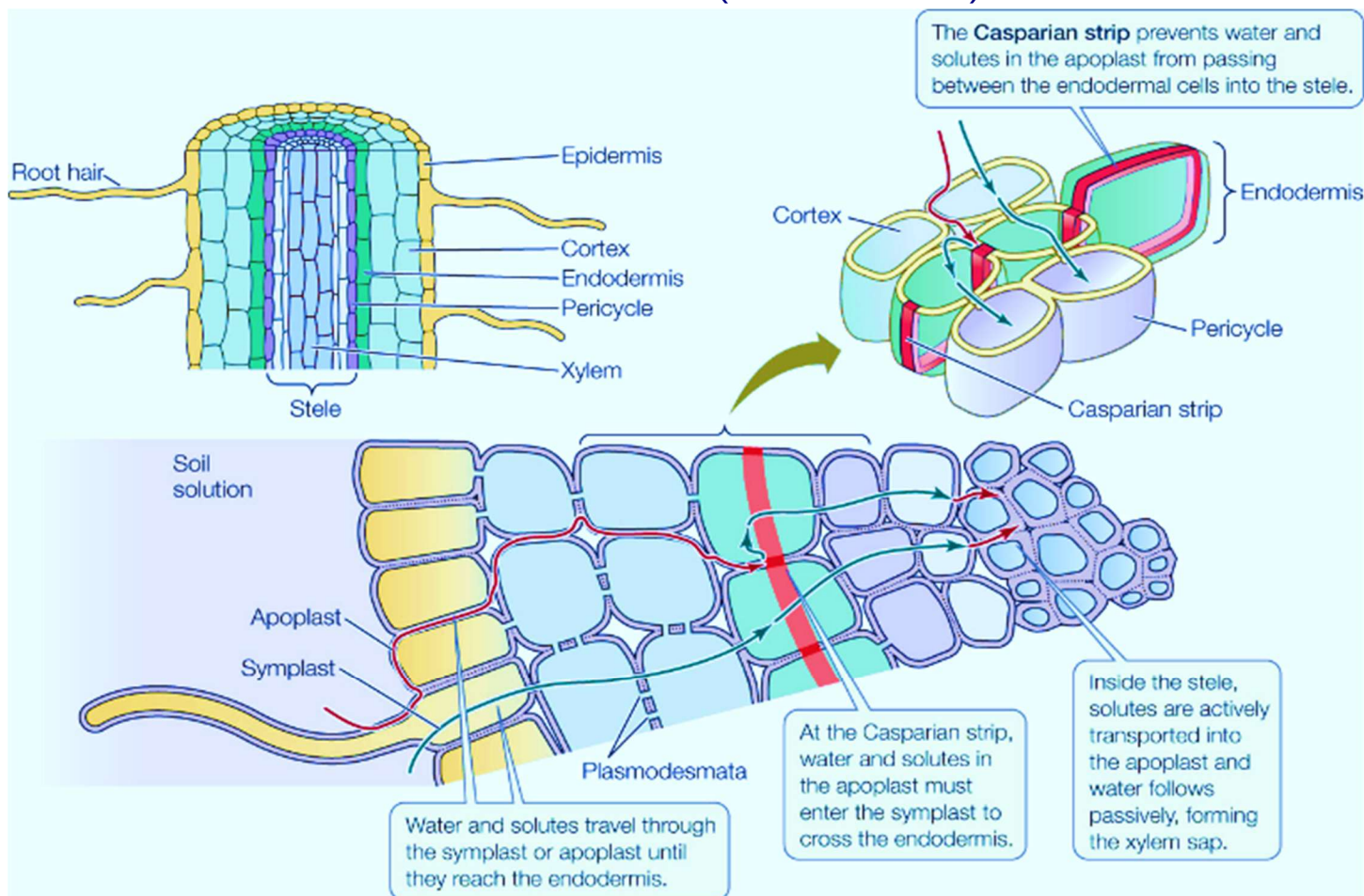


Figure 5: Apoplast and Symplastic Pathways

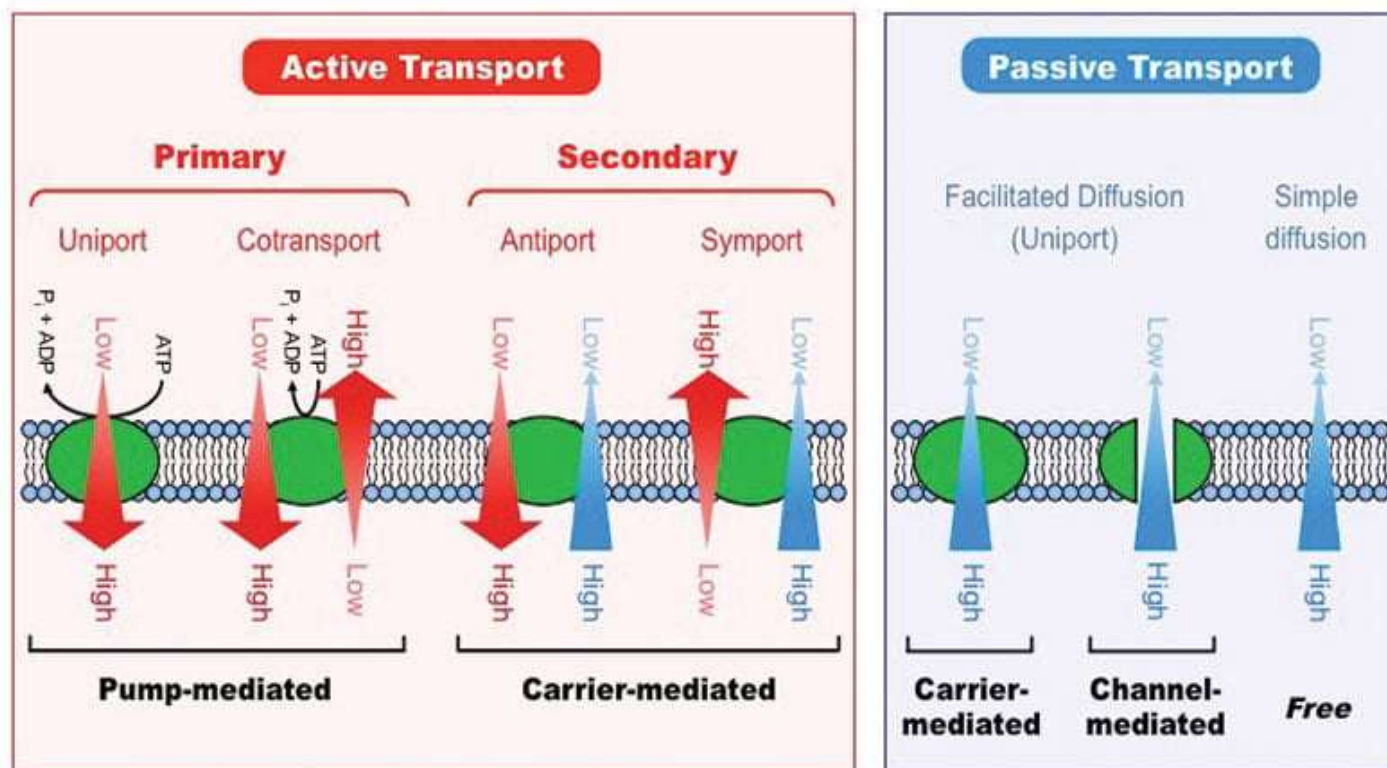


Figure 6: Active and Passive Transport in Plants

However, to reach the xylem and progress towards the upper parts of the plant, water must transition from the apoplast to the symplast. This transition occurs at the endodermis, a specialized layer of cells in the root that acts as a checkpoint. The endodermis regulates the movement of water and solutes into the vascular tissues, ensuring selectivity and control over the substances entering the plant's transport system.

3. Transmembrane (or Vacuolar) Pathway:

The transmembrane or vacuolar pathway involves the movement of water across cell membranes, specifically into and out of the central vacuole. The vacuole is a large, membrane-bound organelle that acts as a storage site for water, ions, and various solutes. Water moves into the vacuole through osmosis, driven by the concentration gradient established between the vacuole and the cytoplasm.

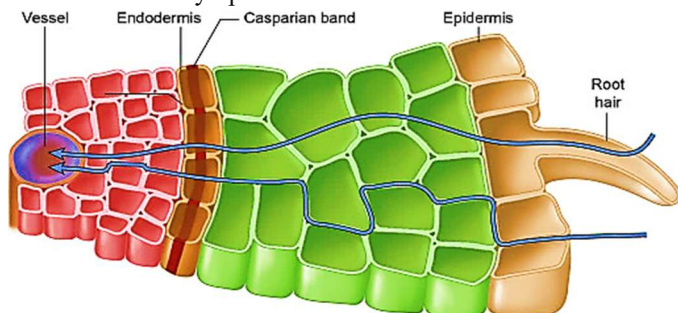


Figure 7: Symplast - an overview

4. Transpiration:

Transpiration is the process by which water evaporates from the leaves of plants, creating a “pull” that helps draw water up the stem from the roots. Transpiration creates a negative pressure (tension) in the xylem vessels, known as the transpiration-cohesion-tension mechanism. This negative pressure helps maintain a continuous column of water from the roots to the leaves, facilitating water absorption and transport.

5. Root Pressure:

Root pressure is the force generated by the active transport of ions into the root cells, which increases the osmotic pressure inside the roots.

Root pressure can contribute to water movement in plants, particularly in situations where transpiration is low, such as during the night.

5. Driving Forces Behind Water Absorption in Plants

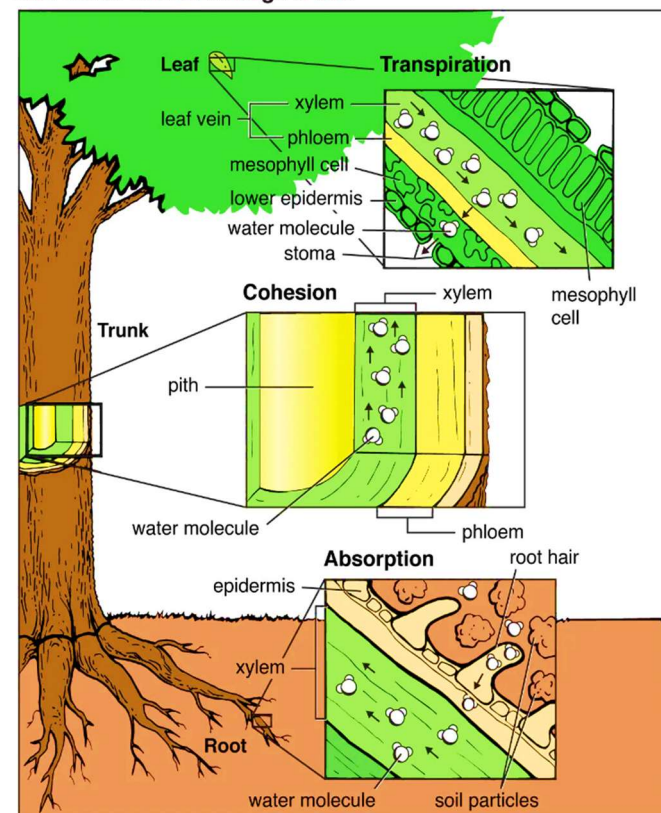
Water absorption in plants is facilitated by several driving forces that work in coordination to ensure the efficient uptake of water from the soil. These driving forces include osmosis, root pressure, capillarity, and the transpiration pull. Let's explore each of these mechanisms in detail:

1. Osmosis:

Osmosis is a fundamental process that plays a central role in water absorption by plant roots. It involves the movement of water molecules across a selectively permeable membrane from an area of lower solute concentration to an area of higher solute concentration. In the context of plants, the root cells actively

pump mineral ions into their cytoplasm, creating a higher solute concentration inside the root cells compared to the surrounding soil. This establishes an osmotic gradient, leading to the influx of water into the roots.

How water moves through a tree



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2. Root Pressure:

Root pressure is a force generated by the active uptake of mineral ions by the root cells. As minerals are actively transported into the roots, water follows through osmosis, resulting in an increase in pressure within the root cells. This root pressure can push water upwards in the xylem, contributing to the movement of water through the plant. However, root pressure is not the primary driving force for long-distance water transport and is more significant in certain plant species and under specific conditions.

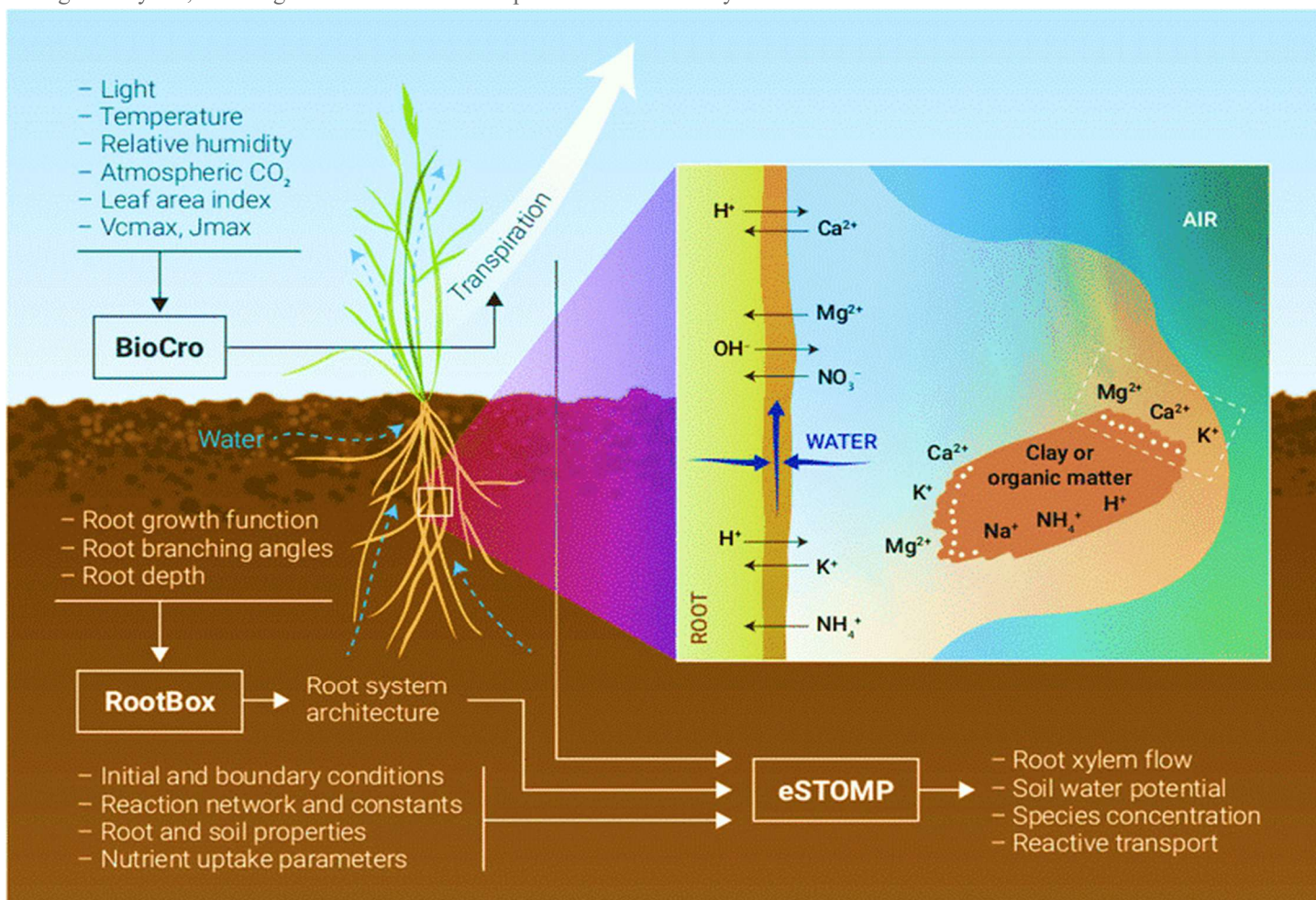
3. Capillarity:

Capillarity is the ability of water to move in narrow spaces, such as the small pores present in the soil and the root hairs of plants. This phenomenon occurs due to the cohesive and adhesive properties of water. Water molecules adhere to each other (cohesion) and to the surfaces of soil particles and root hairs (adhesion), allowing water to move against the force of gravity. Capillarity aids in the initial absorption of water by plant roots from the soil.

4. Transpiration Pull:

The transpiration pull is a crucial force driving the long-distance transport of water in plants. Transpiration is the process by which water vapor escapes from the stomata in the

from the roots and up into the leaves. The cohesion-tension theory explains this process, highlighting the cohesive nature of water molecules and their ability to be pulled up through the xylem



8.1. Means of Transportation in Plants

Plants, being sessile organisms, have evolved various means of transporting substances within their bodies. These means can be broadly categorized into two types:

8.1.1. Xylem: Xylem is a specialized tissue responsible for the transport of water and minerals from the roots to the upper parts of the plant. It consists of dead cells called xylem vessels and tracheids. Water is pulled up through the xylem by the process of transpiration, which is the evaporation of water from the leaves.

Example: In tall trees like the giant sequoia, water can travel up to hundreds of feet through the xylem vessels.

8.1.2. Phloem: Phloem is another specialized tissue responsible for the transport of sugars and other organic compounds from the leaves to the rest of the plant. It consists of living cells called sieve tubes and companion cells. Sugars are transported through the phloem in the form of sucrose.

Example: In sugar maple trees, the phloem transports sucrose from the leaves to the roots, where it is stored as starch.

In addition to these two main types of transport, plants also use other means to move substances within their bodies. These include:

8.2. Diffusion: Diffusion is the movement of molecules from an area of higher concentration to an area of lower concentration. It is a passive process that does not require energy input.

8.3. Cytoplasmic streaming: Cytoplasmic streaming is the movement of cytoplasm within a cell. It is caused by the contraction and relaxation of actin and myosin filaments.

8.4. Plasmodesmata: Plasmodesmata are tiny channels that connect the cytoplasm of adjacent plant cells. They allow for the movement of molecules between cells. These various means of transportation enable plants to distribute water, minerals, and nutrients throughout their bodies, supporting their growth and survival.

9. Driving Forces Responsible for Transportation in Plants

Transportation in plants is driven by transpiration pull (primary), root pressure, cohesion-tension, and active transport. Transpiration, the evaporation of water from stomata, creates a suction that pulls water up xylem vessels, while water potential gradients, capillary action, and cohesion between water molecules maintain the upward flow. Plants are sessile organisms, meaning they cannot move from one place to another. However, they still need to transport water, nutrients, and other substances throughout their bodies. This is accomplished through a variety of mechanisms, including:

9.1. Diffusion: This is the movement of molecules from an area of high concentration to an area of low concentration. Diffusion is responsible for the movement of water and nutrients into and out of plant cells.

9.2. Osmosis: This is the movement of water across a semipermeable membrane from an area of low solute concentration to an area of high solute concentration. Osmosis is responsible for the movement of water into and out of plant cells.

9.3. Active transport: This is the movement of molecules against a concentration gradient, requiring energy input. Active transport is responsible for the movement of nutrients and other substances into and out of plant cells.

9.4. Bulk flow: This is the movement of fluids through a plant in response to a pressure gradient. Bulk flow is responsible for the movement of water and nutrients throughout the plant body.

Examples of Driving Forces Responsible for Transportation in Plants

9.5. Diffusion: The diffusion of water into and out of plant cells is essential for the plant's survival. Water is used for photosynthesis, the process by which plants convert sunlight into energy. Water also helps to transport nutrients throughout the plant body.

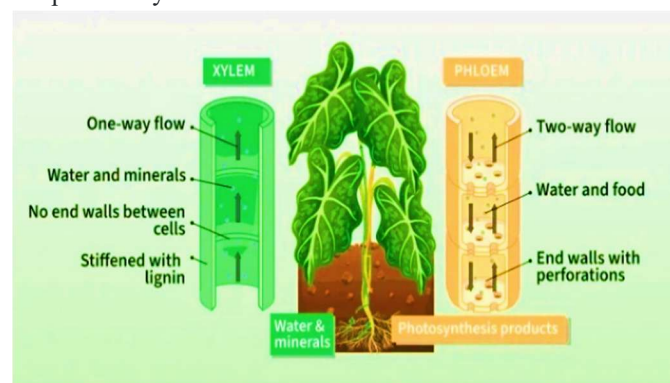


Figure 9: Transportation in plants is the process by which water, minerals, and food move from one part of the plant to another. Just like humans have a circulatory system, plants have their own transport system.

9.6. Osmosis: Osmosis is responsible for the movement of water into and out of plant cells. This is important for maintaining the plant's water balance. When the soil is dry, osmosis helps to move water into the plant's roots. When the soil is wet, osmosis helps to move water out of the plant's roots.

9.7. Active transport: Active transport is responsible for the movement of nutrients and other substances into and out of plant cells. This is important for the plant's growth and development. Active transport helps to move nutrients from the soil into the plant's roots. It also helps to move nutrients from the leaves to the rest of the plant body.

9.8. Bulk flow: Bulk flow is responsible for the movement of water and nutrients throughout the plant body. This is important for the plant's growth and development. Bulk flow helps to move water from the roots to the leaves. It also helps to move nutrients from the roots to the leaves.

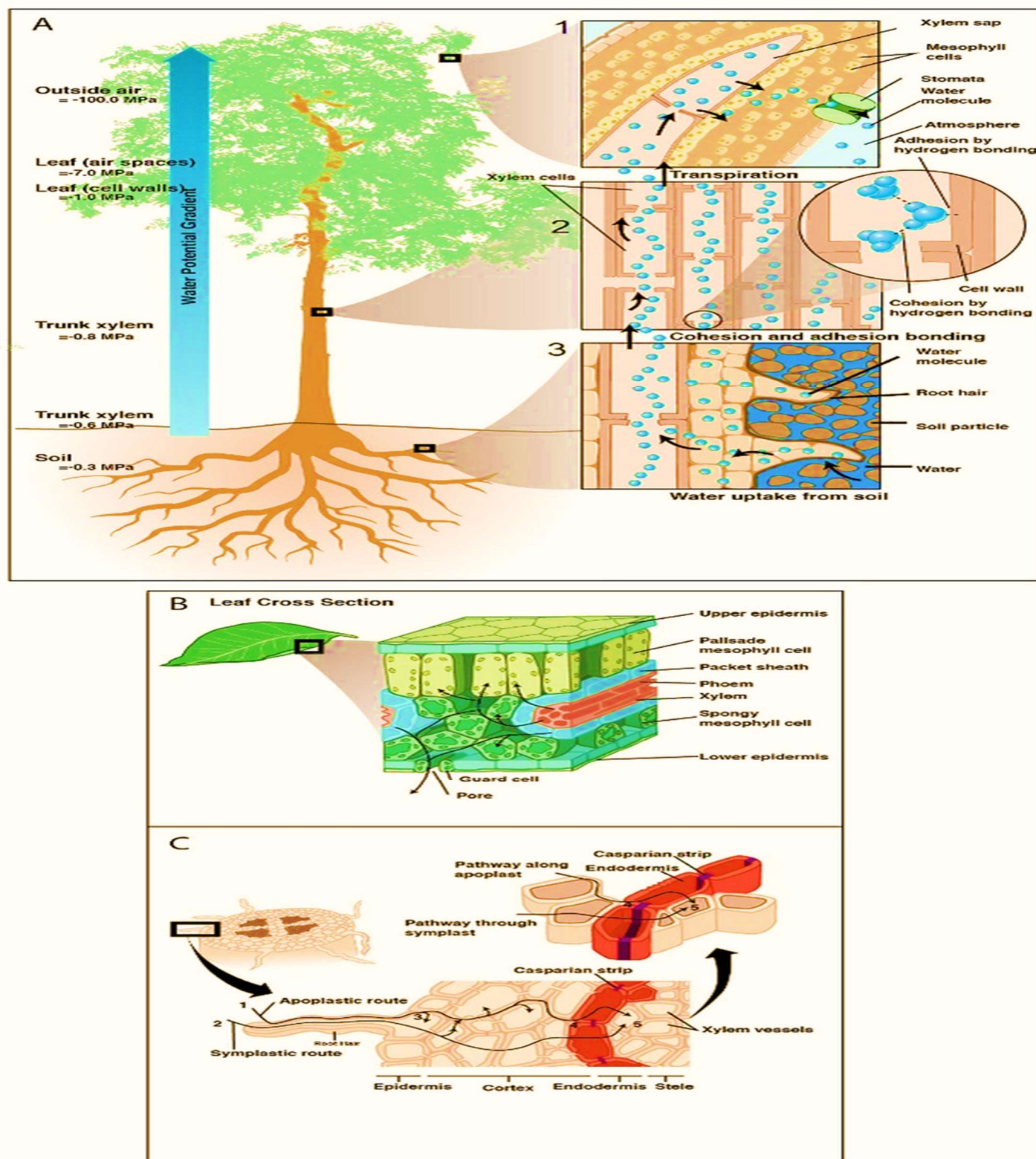


Figure 11: Representation of the water transport pathways along the soil-plant-atmosphere continuum (SPAC). (A) Water moves from areas of high-water potential (i.e., close to zero in the soil) to low water potential (i.e., air outside the leaves). Details of the cohesion-tension mechanism are illustrated with the inset panels (A), where tension is generated by the evaporation of water molecules during leaf transpiration (1) and is transmitted down the continuous, cohesive water columns (2) through the xylem and out the roots to the soil (3). The pathways for water movement out of the leaf veins and through the stomata (B) and across the fine roots (C) are detailed and illustrate both symplastic and apoplastic pathways. Sources: McElrone, A. J., Choat, B., Gambetta, G. A. & Brodersen, C. R. (2013)

Key Concept**1. Introduction**

Plant mineral nutrition is essential for global food security and sustainable agriculture. The processes of nutrient uptake from the soil and their translocation within plants involve complex interactions among soil physicochemical properties, plant physiology, and environmental conditions (Marschner, 2012). Understanding these mechanisms is critical to optimize fertilizer management, improve nutrient use efficiency, and address deficiencies in arid and semi-arid regions.

2. Nutrient Transport from Soil to Roots

Nutrient delivery to the root surface occurs primarily via three mechanisms: mass flow, diffusion, and root interception (Barber, 1995). Mass flow involves transport with the bulk movement of water towards the root due to transpiration, supplying mobile nutrients such as nitrate (NO_3^-), calcium (Ca^{2+}), and magnesium (Mg^{2+}). Diffusion is critical for relatively immobile nutrients such as phosphorus (P) and potassium (K), which move along concentration gradients from bulk soil to the rhizosphere. Root interception contributes less but becomes significant in dense root systems. Root exudates and mycorrhizal associations further enhance nutrient availability by altering rhizosphere chemistry (Smith & Read, 2011).

Mechanism Description: Examples of nutrients

- **Mass flow:** Nutrients move with water flow towards the root driven by transpiration. NO_3^- , Ca^{2+} , Mg^{2+}
- **Diffusion:** Movement along concentration gradients in soil solution. P, K
- **Root interception:** Physical contact of growing roots with soil particles. Ca, Mg, micronutrients

3. Root Uptake Mechanisms

At the root surface, nutrients may follow the apoplastic pathway through cell walls or the symplastic pathway via plasmodesmata. The Casparian strip in the endodermis forces ions to cross membranes before entering the stele, allowing selective uptake (Barber, 2014). Transport proteins, including ion channels, carriers, and H^+ -ATPase-driven pumps, facilitate uptake of macro- and micronutrients (White & Broadley, 2003).

4. Radial Transport and Xylem Loading

Nutrients move radially across root tissues to the xylem through controlled symplastic and apoplastic routes. The Casparian strip ensures selective entry, preventing uncontrolled ion leakage. Xylem loading involves active transport processes, often complexed with organic acids, that determine nutrient flux to the shoot (Marschner, 2012).

5. Long-Distance Transport via Xylem

The cohesion-tension theory explains upward water and nutrient movement through xylem vessels, driven by transpiration from leaves (Venturas et al., 2017). Nutrients such as calcium are particularly dependent on transpiration

flow, resulting in localized deficiencies in low-transpiring tissues such as developing fruits (White & Broadley, 2003). (Schematic representation: Soil → Root uptake → Xylem → Leaf/fruit distribution)

6. Phloem Loading and Redistribution

Sugars and some nutrients are redistributed from source leaves to sink organs (fruits, roots, young leaves) through the phloem, explained by the pressure-flow hypothesis (Turgeon, 2010). Phloem mobility differs among nutrients: nitrogen, phosphorus, and potassium are relatively mobile, while calcium and boron are largely immobile.

Mobile nutrients Immobile nutrients

N, P, K, Mg Ca, Fe, B, Cu, Mn

7. Factors Affecting Nutrient Uptake and Movement

Nutrient dynamics are influenced by soil, plant, and environmental factors. Soil pH regulates nutrient availability, with high pH reducing micronutrient solubility and low pH increasing Al/Fe toxicity (Neina, 2019). Soil moisture and aeration strongly influence mass flow and microbial activity. Plant traits such as root architecture, mycorrhizal associations, and transpiration rate further modulate uptake efficiency (Smith & Read, 2011).

Factor type, examples, effect

- Soil pH, moisture, salinity, organic matter Determines nutrient solubility and mobility
- Plant Root morphology, mycorrhiza, transpiration Affects uptake efficiency and allocation
- Environment Temperature, light, fertilization practices Modulates physiological processes

Conclusion

Nutrient uptake and translocation represent interconnected processes involving soil-plant-environment interactions. While mass flow, diffusion, and root interception govern nutrient supply to the root, membrane transporters and radial barriers regulate entry into the vascular system. Long-distance transport through xylem and phloem ensures nutrient allocation, with mobility differences shaping deficiency patterns. Understanding these mechanisms underpins nutrient management strategies to enhance crop productivity and sustainability in diverse agroecosystems.

10. Theories of Ion Uptake in Plants

The theories are the following: 1. Lundegardh Theory 2. Contact Exchange Theory 3. Carbonic Acid Exchange Theory 4. Bennet-Clark's Protein Lecithin Theory 5. Donnan's Equilibrium Theory.

1. Lundegardh Theory (Electro-Chemical Theory) of Ion Uptake:

Lundegardh (1945) proposed that an electrical potential gradient existing between the cell membrane of plants and the outside solution is responsible for the passage of electrons from the inside solution (cytoplasm) to the outside membrane

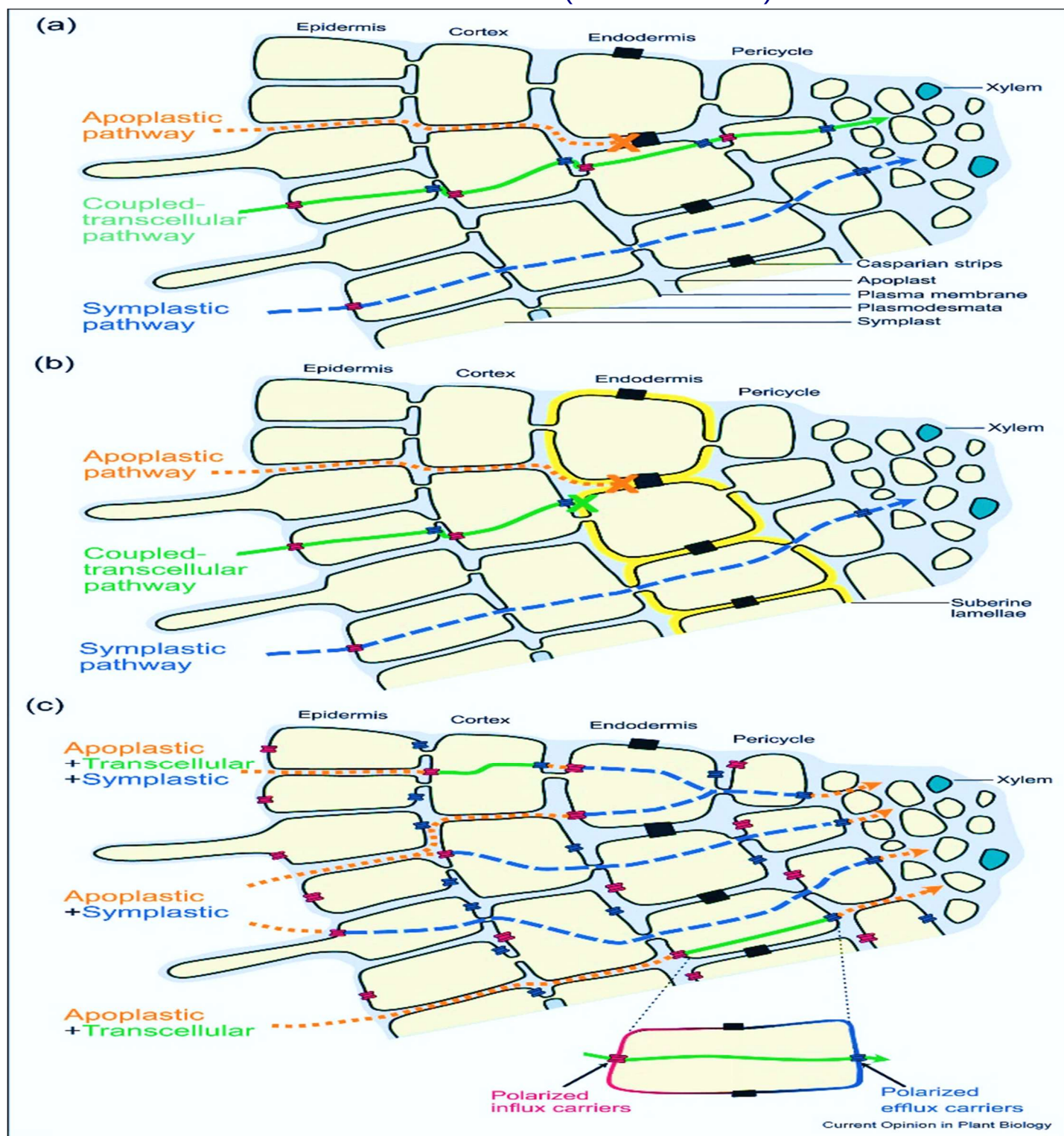


Figure:12. Theoretical pathways for radial transport of nutrients in Arabidopsis root (transversal view). (a) Schematic representation of nutrients' radial transport in Arabidopsis root after CS establishment (state I endodermis differentiation). The apoplastic pathway is blocked by the CS at the endodermis. (b) Schematic representation of nutrients' radial transport in Arabidopsis root after CS establishment and suberine lamellae deposition (state II endodermis differentiation). The suberine lamellae blocks the diffusion into the endodermal symplast and is predicted to block the transcellular pathway. (c) The combination and interconnection of the three pathways along the root cell layers allow an efficient radial transport of nutrients in the root. The transcellular pathway is facilitated by polarized influx and efflux carriers. The chemical properties of the nutrients, the physiology of the plant and the root development stage influence the pathway of nutrient transport. Source: Panel Kevin Robe, Marie Barberon. 2023, Volume 74, August 2023, 102376. <https://doi.org/10.1016/j.pbi.2023.102376>

(apoplasm). Such flow or passage of electrons causes movement of anions from outside to inside. The Lundegardh theory, also known as the cytochrome pump theory or electrochemical theory, proposes that anion absorption is an active process linked to respiration, while cation absorption is passive. It posits that an electrochemical gradient created by electron transport (cytochromes) drives anions across the membrane, with anions and cations being absorbed independently.

An oxygen deficit in the cytoplasm of a plant cell induced by respiration is responsible for a drop in the redox potential of the cytoplasm. It is believed that cytochromes (Fe-containing substances) are present on the outer membrane, where Fe is present in Fe^{3+} form because of higher redox potential when these cytochromes move through thermal motion across the membrane.

1.1. Key Aspects of the Lundegardh Theory

1. Anion Respiration: Lundegardh observed that when a plant is moved from water to a salt solution, respiration rates increase, a phenomenon labeled "salt respiration" or "anion respiration."

2. Cytochrome Pump: The theory holds that anions (A^-) are actively transported across the membrane through the cytochrome chain, specifically involving redox changes in cytochromes.

1.2. Mechanism of Ion Movement:

1.2.1. Anion Uptake: Cytochrome oxidase on the inner surface reduces iron, releasing the anion into the cell. Oxidation occurs on the outer surface, allowing anion pickup.

1.2.2. Cation Uptake: Cations (C^+) move passively into the cell along the electrochemical gradient created by the increased negative charge from accumulated anions.

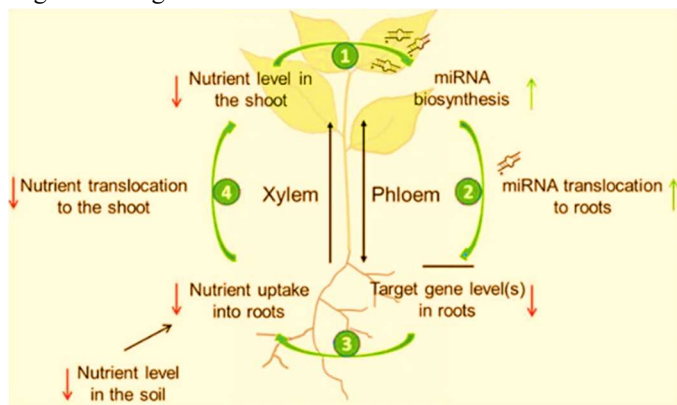


Figure 13: Ion Uptake Mechanism (Contact Exchange Theory, CO_2 Exchange Theory)

1.2.3. Anion-specific: The theory explains anion accumulation in detail but is less applicable to cation absorption, as detailed in this overview of plant nutrient ion uptake theories. Fe^{3+} is reduced to Fe^{2+} by the acquisition of electrons from the respiratory chain. In the outside membrane, Fe of cytochrome is oxidised by losing an electron, which

combines with H^+ to form water. Outward flow of the electron is balanced by the counter movement of anions into the cell. Lundegardh deduced that since the cytoplasm of the cell is negatively charged compared to the outside, energy must be required in pumping anions into the cytoplasm, and cations move along with anions to maintain a balance between anions and cations.

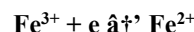
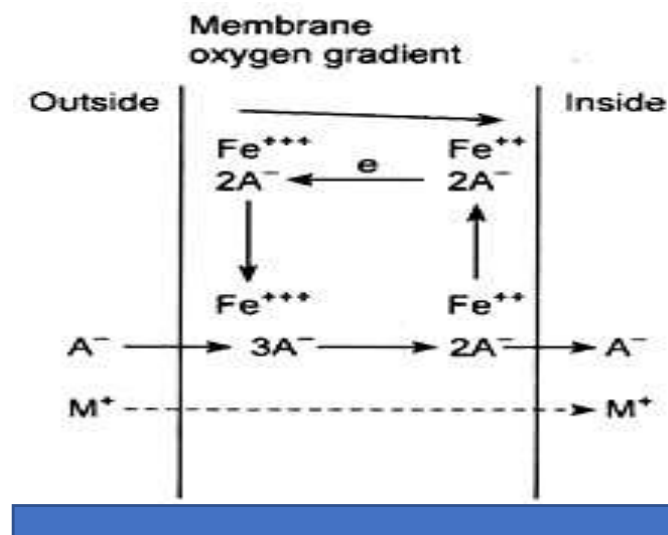


Figure 14: However, the hypothetical scheme of the Lundegardh theory in figures.

Limitations of:

- (i) Cytochromes are not located in the cell wall of plants, and
- (ii) Ideally, four anion molecules should move in response to the consumption of one molecule of O_2 , but actually, this number is much higher.

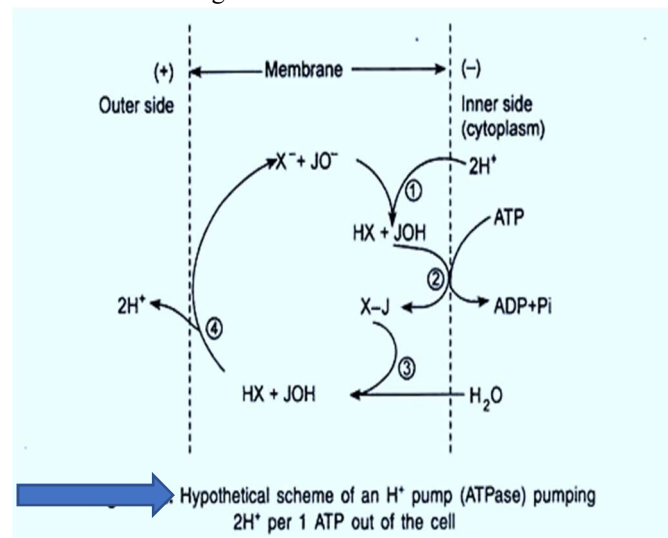


Figure 14. Hypothetical scheme of an H^+ pump (ATPase)

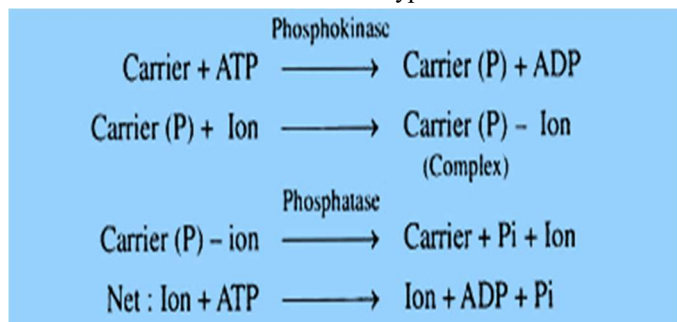
2. Carrier Hypothesis of Ion Uptake:

In 1953, Epstein proposed the carrier hypothesis to describe primarily the active accumulations of ions across the cell membrane. According to this hypothesis, there is a carrier present on the membrane, which, combined with the ion at the

outer surface of the plasma membrane, forms a carrier-ion complex that traverses the membrane, which is relatively impermeable to the ion alone.

On the inner side of the membrane, due to some chemical changes, the membrane-ion complex breaks, releasing the ion, which cannot leak because the membrane is impermeable to free ions. On releasing the ion, the carrier moves back to the outer surface of the membrane where it can again combine with an ion.

Usually, the carrier can take up ions only in the phosphorylated form, and on the inside of the membrane, both phosphate and ions are released. Metabolic energy is required for the accumulation of ions in the carrier hypothesis.



The carrier hypothesis can explain:

- (a) An accumulation of salts against the concentration gradient,
- (b) The specificity in ion uptake usually found in all plants, and
- (c) The transport of ions through membranes, which by themselves are impermeable.

Chemically, this cycle has been proposed by Mengel and Kirkby (1982) as follows: However, schematically the carrier ion transport is depicted as follows:

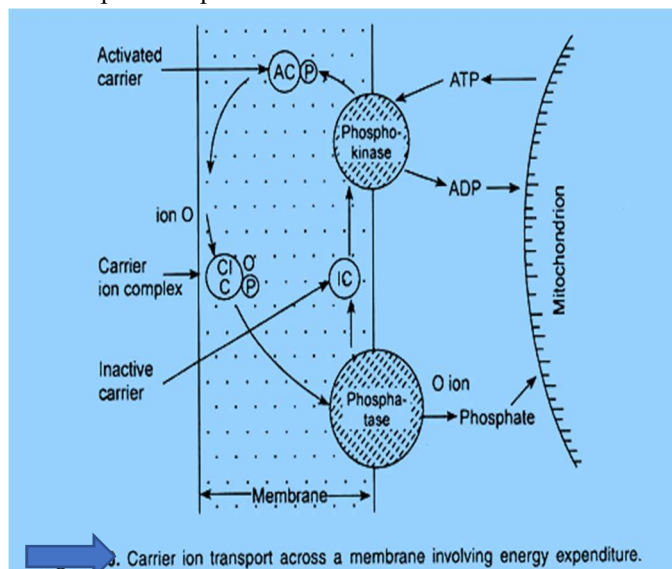


Figure 15: Carrier ion transport across a membrane involving energy expenditure

2. Contact Exchange Theory of Ion Uptake:

According to this theory, the ions adsorbed on the surface of roots cells and clay particles are not held tightly but oscillate within small volume of space.

If the roots and clay particles are in close contact with each other, the oscillation volume of ions absorbed on root surface may overlap with the oscillation volume of ions adsorbed on clay particles, and the ions adsorbed on clay particle may be exchanged with the ions adsorbed on root surface directly without first being dissolved in soil solution.

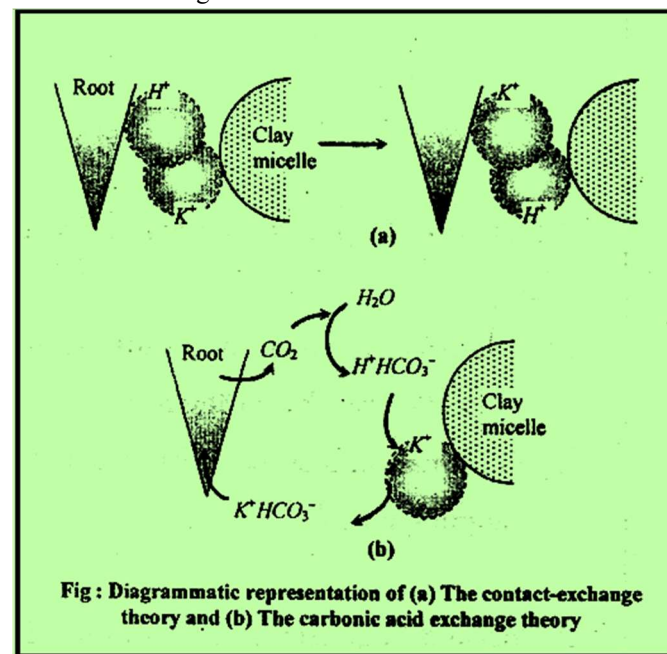


Figure 16: Diagrammatic representation of a) The contact exchange theory b) The carbonic exchange theory

3. Carbonic Acid Exchange Theory of Ion Uptake:

According to this theory, the CO_2 released during respiration of root cells combines with water to form carbonic acid (H_2CO_3). Carbonic acid dissociates into H^+ and an anion, HCO_3^- , in soil solution. These H^+ ions may be exchanged for cations adsorbed on the clay particles. The cations thus released into the soil solution from the clay particles may be adsorbed on root cells in exchange for H^+ ions or as in ion pairs with bicarbonate. Thus, the soil solution plays an important role in carbonic acid exchange theory.

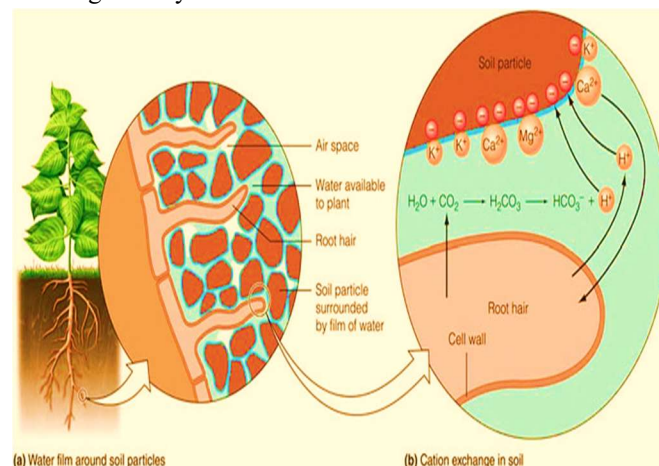


Figure 17: a.) water around soil particle b.) Cation exchange in soil.

4. Bennet-Clark's Protein Lecithin Theory of Ion Uptake:

In 1856, Bennet-Clark suggested that because the cell membranes of plants chiefly consist of phospholipids and proteins and certain enzymes seem to be located on them, the carrier could be a protein associated with the phosphatide called as lecithin. He also assumed the presence of different phosphatides to correspond with the number of known competitive groups of cations and anions.

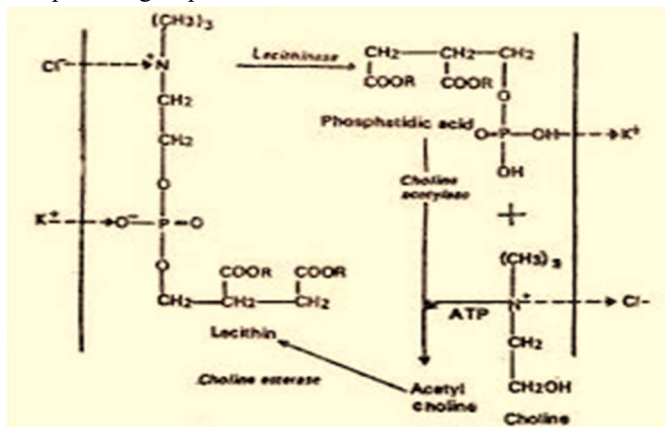


Figure 18: Bennet-Clark's Protein Lecithin Theory of Ion Uptake

According to this theory:

1. The Phosphate group in the phosphatide is regarded as the active center binding the cations and the basic choline group as the anion binding center.
2. The ions are liberated on the inner surface of the membrane by decomposition of lecithin by the enzyme lecithinase.
3. The regeneration of the carrier lecithin from phosphatidic acid and choline takes place in the presence of the enzyme choline acetylase and choline esterase and ATP. The latter acts as a source of energy.

5. Donnan's Equilibrium Theory of Ion Uptake:

Donnan equilibrium (also called Gibbs-Donnan equilibrium) refers to the imbalance of ion species across two solutions separated by an interface that prevents at least one species to pass through (Donnan, 1924). The interface could be a semipermeable membrane, or between a polyelectrolyte polymer gel and its surrounding solution (Brannon-Peppas and Peppas, 1991), or between two different polymer gels (Ohki, 1965; Guo et al., 2016). There are two key phenomena that are often associated with the Donnan equilibrium: osmotic pressure and Donnan potential.

The former is a pressure difference across the membrane or interface and the latter is an electrical potential difference between the two liquids. These two phenomena are observed and exploited in a wide range of systems and technologies, from biology (Sperelakis, 2001; McLaughlin, 1989) to desalination (Mohammad et al., 2015) to batteries and fuel cells (Knehr and Kumbur, 2011).

Donnan established relationships between ion concentrations in the two regions at equilibrium (Donnan, 1924; 1955), which can

be combined with the charge neutrality requirement to solve for the concentrations of the ions in each region. Once the concentrations are known, one can easily calculate the osmotic pressure from van't Hoff's law and the Donnan potential from the ion concentration ratio. Donnan equilibrium criteria are widely used in different fields such as cell biology (Sperelakis, 2001; McLaughlin, 1989), membrane desalination (Greenlee et al., 2009), and polyelectrolyte hydrogel expansion (Flory, 1953).

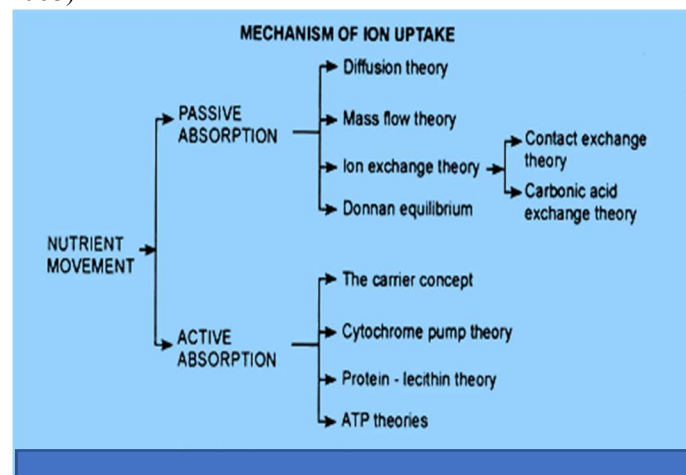


Figure: An Overall Scheme for Ion Uptake

The accumulation of ions inside the cells without involving expenditure of the metabolic energy can be explained to some extent by Donnan's equilibrium theory.

According to this theory, there are certain pre-existing ions inside the cell that cannot diffuse outside through membrane. Such ions are called as in diffusible or fixed ions. However, the membrane is permeable to both anions and cations of the outer solutions.

Suppose there are certain fixed anions in the cell that is in contact with an outer solution containing anions and cations. Normally equal number of anions and cations would have diffused into the cell through an electrical potential to balance each other, but to balance the fixed anions more cations will diffuse into the plant cell.

This equilibrium is known as Donnan's equilibrium. In this particular case, there would be an accumulation of cations inside the cell. If, however, there are fixed cations inside the plant cell, the Donnan's equilibrium will result in the accumulation of anions inside the plant cell.

Based on recent research trends (2024-2026), the chemistry of nutrient transport in plants is moving beyond basic uptake mechanisms toward understanding molecular regulation, stress responses, and nanotechnology-based delivery systems.

Here are the top new research topics regarding the chemistry of nutrient transportation in plants:

1. Nanoparticle-Mediated Nutrient Delivery and Transport
Targeted Micronutrient Transport: Investigating how engineered nano-fertilizers (e.g., zinc oxide, iron oxide,

hydroxyapatite) move through the cuticle and root plasma membrane to improve bioavailability.

Nanoparticle Tracking in Vascular Tissue: Utilizing fluorescence imaging to trace the movement of nutrient-loaded nanoparticles through xylem and phloem, particularly under abiotic stress.

Chemical Modification for Controlled Release: Developing chitosan or polymer-coated nanocarriers that release nutrients in response to root exudate chemistry (pH or organic acids).

2. Molecular Chemistry of Transporters and Sensing

Nutrient Transporter "Sensing" Mechanisms: Researching how transporters, such as NRTs (nitrate transporters) and PHTs (phosphate transporters), act as sensors to trigger signaling pathways upon nutrient detection.

Post-Translational Modification of Transporters: Studying how phosphorylation or ubiquitination of membrane proteins alters the chemical efficiency of nutrient transport under stress.

Polarized Transport in Root Architecture: Exploring the role of localized nutrient carriers at the plasma membrane and their response to changing soil chemical properties.

3. Phloem-Xylem Loading and Long-Distance Transport

Metal-Chelate Transport Complexes: Analyzing the chemical form (e.g., EDTA or natural organic complexes) in which micronutrients (Fe, Zn, Cu) are translocated within the phloem.

Regulatory Signaling in Phloem Flow: Investigating the role of small signaling molecules (miRNAs, peptides, and hormones) in controlling the redirection of nutrients under nutrient-deficient conditions.

4. Soil-Root Interface Chemistry (Rhizosphere)

Organic Acid Exudation Mapping: Using new techniques to analyze how root exudates alter the chemical environment to dissolve insoluble nutrients for improved transport.

Mycorrhizal-Mediated Transport Networks: Exploring the chemical dialogue between fungi and roots to facilitate the transport of immobile nutrients in arid soil.

5. Smart Nutrient Management Using Omics

Transcriptomics of Transport: Mapping the gene expression of transporters to understand how plants, particularly in vertical farming or high-light conditions, regulate nutrient uptake.

Metabolomics of Nutrient Assimilation: Investigating the metabolic pathways that consume absorbed nutrients to drive further transport in high-yield crops

Factors affecting salt absorption

I. External factors

(i) Temperature: Absorption of salt is affected by change in temperature. In general, an increase in temperature results in increased absorption of salts up to a certain optimum level. At higher temperature, the absorption is inhibited. The change in the temperature also affects the processes of diffusion.

(ii) pH: Change of pH of the soil solution affects the availability of ions to the plants. Decrease in the pH of soil solution accelerates the absorption of anions but increase in pH will

favour the absorption of cations. However, pH beyond the optimum level (higher or lower) may damage the plant tissues and inhibit the salt absorption.

(iii) Light: It has no direct effect, but indirectly affecting the transpiration and photosynthesis so that the salt absorption is affected

(iv) Oxygen: Absence of oxygen will inhibit the active salt absorption.

(v) Interaction: The absorption of one ion is influenced by the presence of other ions in the medium. Viets (1944) demonstrated that the absorption of potassium is affected by the presence of calcium, magnesium and other polyvalent cations in the soil solution. Epstein (1978) demonstrated the interaction of several ions as competitors for binding sites on carriers.

II. Internal factors

(i) Growth: Cell division, elongation and developmental processes promote the absorption of salt.

(ii) Aging: As the root matures, it increases the surface area, which is favorable for salt absorption. Transport of Minerals Both xylem and phloem take part in the transport of mineral salts. Upward movement from roots to the shoot occurs through xylem. Both upward and downward movement from mature leaves occur through phloem. Translocation of salts in the xylem the minerals for the most part is transported in the xylem. The transport of minerals in the xylem occurs along with the transpiration stream. Analysis of xylem sap also shows the presence of large amount of dissolved salts. These include not only inorganic salts but organic compounds of nitrogen and phosphorus. Such organic compounds are largely responsible for the movement of nitrogen and phosphorus. A radioactive experiment was conducted by Stout and Hoagland (1939) to prove the upward movement of salts through xylem. The experiment was carried out on a willow plant. The xylem and phloem were carefully separated from each other along a 9-inch length of willow stem. A sheet of paraffined paper was inserted between the two tissues. Then, potassium K42 was fed to the plant via the nutrient solution. Practically, all the tracer elements were found in the xylem which shows that upward transport occurred in the xylem. Above and below the stripped area there were considerable amounts of K42 in both xylem and phloem. This indicates the lateral transfer of salts into phloem. Lateral transport Some of the minerals are transferred radially from xylem to the phloem mainly through parenchymatous cells. They are also transported to other tissues where they accumulate in the living cells. Translocation of salts in the phloem Minerals are transported through phloem also. The translocation in phloem mainly occurs from the leaves just before abscission. These minerals which move out of the leaf before abscission are nitrogen, potassium, phosphorus, sulphur and chlorine. The movement of ions in the phloem occurs both upward and downward into the younger leaves and to apical regions of stem and root. Mechanism of Translocation The

absorbed ions diffuse freely into the root across the epibema, cortex and finally reach the endodermis. Further movement is retarded by the casparian strip present in the endodermis. The movement of minerals across the living tissues does not require metabolic energy. The ions are passively translocated through the wet cell walls and plasmodesmata of the cortex and to the endodermis. Then, the ions are released into the xylem from the endodermis. This is called the symplast theory of ion uptake. The ion movement from endodermis to xylem elements is an active process. It requires the involvement of metabolic energy, which comes from respiration. The concentration of xylem sap remains usually greater than those of the surrounding cells. It requires extra energy because the ion movement from endodermis to xylem is against the concentration gradient. Due to special Casparian strips, the ions are directly diffused to xylem elements. Involvement of special cells called transfer cells in the movement of salts into the xylem elements has been suggested by Gunning (1972). The minerals entering into xylem are translocated upward along the transpiration stream. The minerals are radially transported into phloem through the cambial cells. Some of the minerals are still transported through phloem along with the organic solutes and some of them accumulate in the living tissues of parenchyma. Transfer Cells: The transfer cells are special cells, which take part in transmembrane flux of solutes. Transfer cells found in the xylem facilitate mineral absorption.

11. TRANSPORT OF WATER AND MINERAL IONS IN PLANTS From both a physiological and a structural point of view, transport activities in the plant may be divided into two parts.

1. Transport of water and nutrients through cells. Examples of this include the movement of water from the soil solution through root cells to the vascular system and the movement of water from the vascular system through leaf cells to the intercellular spaces. Water moves for only short distances through cells. Short-distance transport, which is important in cell to cell interactions, probably takes place mostly by diffusion through plasmodesmata. In some cases, short-distance transport is an active process requiring energy expenditure by the cells.

2. Transport between roots and leaves. Long-distance movement of water and nutrients is mainly through the xylem tracheids and vessels and the phloem sieve elements of the vascular system. The xylem tracheids and vessels, which are dead cells, can be envisioned as a series of water-filled tubes. In herbaceous plants the distance of water movement through the xylem may be only centimeters while in trees the water may move through this system over 110 meters. The aqueous phase that lies outside of the cellular membrane (e.g. cell walls and the conducting cells of the xylem) are considered to represent the apoplast.

Have you ever wondered how water reaches the top of tall trees, or for that matter how and why substances move from one cell to the other, whether all substances move in a similar way, in the same direction and whether metabolic energy is required for moving substances? Plants need to move molecules over very long distances, much more than animals do; they also do not have a circulatory system in place. Water taken up by the roots has to reach all parts of the plant, up to the very tip of the growing stem. The photosynthates, or food synthesized by the leaves have also to be moved to all parts including the root tips embedded deep inside the soil. Movement across short distances, say within the cell, across the membranes, and from cell to cell within the tissue has also to take place. To understand some of the transport processes that take place in plants, one would have to recollect one's basic knowledge about the structure of the cell and the anatomy of the plant body. We also need to revisit our understanding of diffusion, besides gaining some knowledge about chemical potential and ions. When we talk of the movement of substances we need first to define what kind of movement we are talking about, and also what substances we are looking at. In a flowering plant the substances that would need to be transported are water, mineral nutrients, organic nutrients and plant growth regulators. Over small distances substances move by diffusion and by cytoplasmic streaming supplemented by active transport. Transport over longer distances proceeds through the vascular system (the xylem and the phloem) and is called translocation. An important aspect that needs to be considered is the direction of transport. In rooted plants, transport in xylem (of water and minerals) is essentially unidirectional, from roots to the stems. Organic and mineral nutrients however, undergo multidirectional transport. Organic compounds synthesized in the photosynthetic leaves are exported to all other parts of the plant including storage organs. From the storage organs they are later re-exported. The mineral nutrients are taken up by the roots and transported upwards into the stem, leaves and the growing regions. When any plant part undergoes senescence, nutrients may be withdrawn from such regions and moved to the growing parts. Hormones or plant growth regulators and other chemical signals are also transported, though in very small amounts, sometimes in a strictly polarized or unidirectional manner from where they are synthesized to other parts. Hence, in a flowering plant there is a complex traffic of compounds (but probably very orderly) moving in different directions, each organ receiving some substances and giving out some others.

11.1 MEANS OF TRANSPORT

11.1.1 Diffusion

Movement by diffusion is passive, and may be from one part of the cell to the other, or from cell to cell, or over short distances, say, from the intercellular spaces of the leaf to the outside. No energy expenditure takes place. In diffusion, molecules move

in a random fashion, the net result being substances moving from regions of higher concentration to regions of lower concentration. Diffusion is a slow process and is not dependent on a 'living system'. Diffusion is obvious in gases and liquids, but diffusion in solids is more likely rather than of solids. Diffusion is very important to plants since it is the only means for gaseous movement within the plant body.

Diffusion rates are affected by the gradient of concentration, the permeability of the membrane separating them, temperature and pressure.

11.1.2 Facilitated Diffusion

As pointed out earlier, a gradient must already be present for diffusion to occur. The diffusion rate depends on the size of the substances; obviously smaller substances diffuse faster. The diffusion of any substance across a membrane also depends on its solubility in lipids, the major constituent of the membrane. Substances soluble in lipids diffuse through the membrane faster. Substances that have a hydrophilic moiety, find it difficult to pass through the membrane; their movement has to be facilitated. Membrane proteins provide sites at which such molecules cross the membrane. They do not set up a concentration gradient: a concentration gradient must already be present for molecules to diffuse even if facilitated by the proteins. This process is called facilitated diffusion.

In facilitated diffusion special proteins help move substances across membranes without expenditure of ATP energy. Facilitated diffusion cannot cause net transport of molecules from a low to a high concentration - this would require input of energy. Transport rate reaches a maximum when all of the protein transporters are being used (saturation). **Facilitated diffusion is very specific:** it allows cell to select substances for uptake. It is sensitive to inhibitors which react with protein side chains.

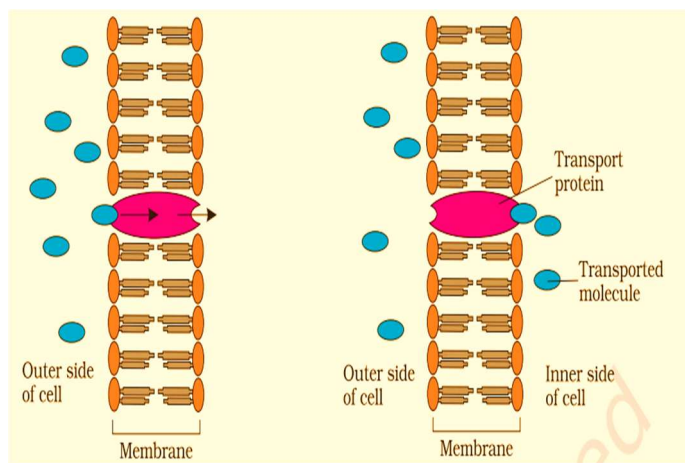


Figure 19: The proteins form channels in the membrane for molecules to pass through. Some channels are always open; others can be controlled. Some are large, allowing a variety of molecules to cross. The porins are proteins that form large Uniport A pores in the outer membranes of the plastids, mitochondria and some bacteria allowing molecules up to the

size of small proteins to pass through. Figure shows an extracellular molecule bound to the transport protein; Antiport the transport protein then rotates and releases the molecule inside the cell, e.g., water channels - made up of eight different types of aquaporins.

11.1.4. Passive symports and antiport

Some carrier or transport proteins allow diffusion only if two types of molecules move together. In a symport, both molecules cross the membrane in the same direction; in an antiport, they move in opposite directions. When a molecule moves across a membrane independent of other molecules, the process is called uniport.

11.1.5. Active Transport

Active transport uses energy to transport and pump molecules against a concentration gradient. Active transport is carried out by specific membrane-proteins. Hence different proteins in the membrane play a major role in both active as well as passive transport. Pumps are proteins that use energy to carry substances across the cell membrane. These pumps can transport substances from a low concentration to a high concentration ('uphill' transport). Transport rate reaches a maximum when all the protein transporters are being used or are saturated. Like enzymes the carrier protein is very specific in what it carries across the membrane. These proteins are sensitive to inhibitors that react with protein side chains.

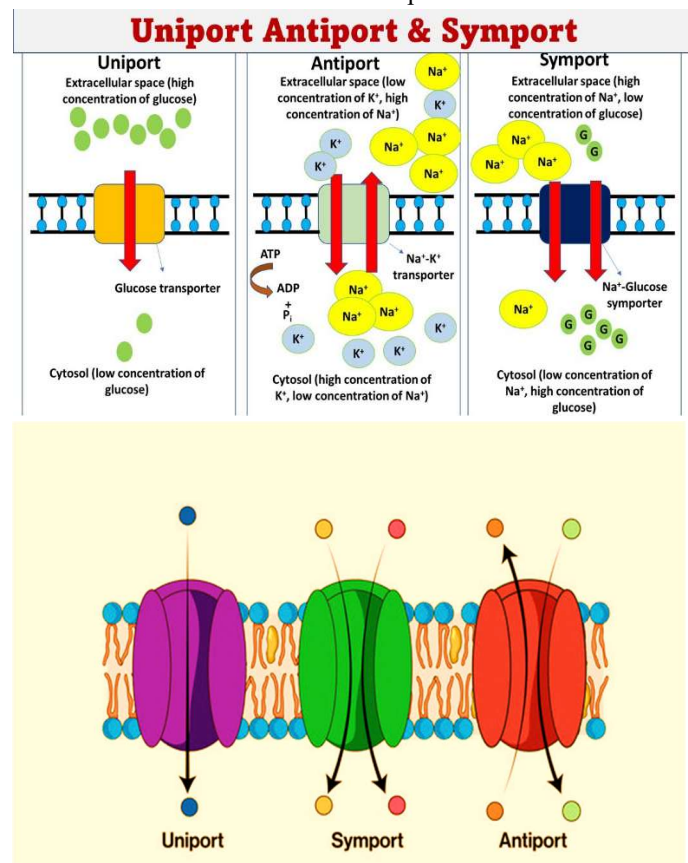


Figure 19: Uniport and symport movements of Ion through plasma membrane.

11.1.6. Comparison of Different Transport Processes

Table gives a comparison of the different transport mechanisms. Proteins in the membrane are responsible for facilitated diffusion and active transport and hence show common characteristics of being highly selective; they are liable to saturate, respond to inhibitors and are under hormonal regulation. But diffusion whether facilitated or not - take place only along a gradient and do not use energy.

11.2. PLANT-WATER RELATIONS

Water is essential for all physiological activities of the plant and plays a very important role in all living organisms. It provides the medium in which most substances are dissolved. The protoplasm of the cells is nothing but water in which different molecules are dissolved and (several particles) suspended. A watermelon has over 92 per cent water; most herbaceous plants have only about 10 to 15 per cent of its fresh weight as dry matter. Of course, distribution of water within a plant varies - woody parts have relatively very little water, while soft parts mostly contain water. A seed may appear dry but it still has water - otherwise it would not be alive and respiring!

Property	Simple Diffusion	Facilitated Transport	Active Transport
Requires special membrane proteins	No	Yes	Yes
Highly selective	No	Yes	Yes
Transport saturates	No	Yes	Yes
Uphill transport	No	No	Yes
Requires ATP energy	No	No	Yes

Terrestrial plants take up huge amount water daily but most of it is lost to the air through evaporation from the leaves, i.e., transpiration. A mature corn plant absorbs almost three liters of water in a day, while a mustard plant absorbs water equal to its own weight in about 5 hours. Because of this high demand for water, it is not surprising that water is often the limiting factor for plant growth and productivity in both agricultural and natural environments.

11.2.1 Water Potential

To comprehend plant-water relations, an understanding of certain standard terms is necessary. Water potential is a concept fundamental to understanding water movement. Solute potential and pressure potential are the two main components that determine water potential term molecules possess kinetic energy. In liquid and gaseous form, they are in random motion that is both rapid and constant. The greater the concentration of water in a system, the greater is its kinetic energy or 'water potential'. Hence, it is obvious that pure water will have the greatest water potential. If two systems containing water are in contact, random movement of water molecules will result in net movement of water molecules from the system with higher energy to the one with lower energy. Thus, water will move from the system containing water at higher water potential to

the one having low water potential. This process of movement of substances down a gradient of free energy is called diffusion. Water potential is denoted by the Greek symbol Psi or Ψ and is expressed in pressure units such as pascals (Pa). By convention, the water potential of pure water at standard temperatures, which is not under any pressure, is taken to be zero.

If some solute is dissolved in pure water, the solution has fewer free water molecules and the concentration (free energy) of water decreases, reducing its water potential. Hence, all solutions have a lower water potential than pure water; the magnitude of this lowering due to dissolution of a solute is called solute potential or Ψ_s is always negative. The more the solute molecules, the lower (more negative) is the. For a solution at atmospheric pressure (water potential) = (solute potential).

If a pressure greater than atmospheric pressure is applied to pure water or a solution, its water potential increases. It is equivalent to pumping water from one place to another. Can you think of any system in our body where pressure is built up? Pressure can build up in a plant system when water enters a plant cell due to diffusion causing a pressure built up against the cell wall, it makes the cell turgid (see section 11.2.2); this increases the pressure potential. Pressure potential is usually positive, though in plants negative potential or tension in the water column in the xylem plays a major role in water transport up a stem. Pressure potential is denoted as Ψ_p . Water potential of a cell is affected by both solute and pressure potential. The relationship between them is as follows:

11.2.2 Osmosis

The plant cell is surrounded by a cell membrane and a cell wall. The cell wall is freely permeable to water and substances in solution hence is not a barrier to movement. In plants the cells usually contain a large central vacuole, whose contents, the vacuolar sap, contribute to the solute potential of the cell. In plant cells, the cell membrane and the membrane of the vacuole, the tonoplast together are important determinants of movement of molecules in or out of the cell.

Osmosis is the movement of water

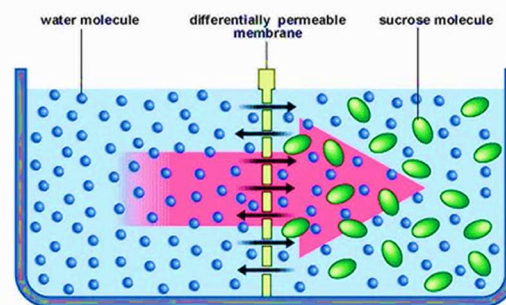


Image from askwillonline.com

Figure 20: Osmosis processes through semi permeable membrane

Osmosis is the term used to refer specifically to the diffusion of water across a differentially- or selectively permeable membrane. Osmosis occurs spontaneously in response to a driving force. The net direction and rate of osmosis depends on both the pressure gradient and concentration gradient. Water will move from its region of higher chemical potential (or concentration) to its region of lower chemical potential until equilibrium is reached. At equilibrium the two chambers should have nearly the same water potential.

You may have made a potato osmometer in your earlier classes in school. If the potato tuber is placed in water, the water enters the cavity in the potato tuber containing a concentrated solution of sugar due to osmosis. Study Figure in which the two chambers, A and B, containing solutions are separated by a semi-permeable membrane.

- Solution of which chamber has a lower water potential?
- Solution of which chamber has a lower solute potential?
- In which direction will osmosis occur?
- Which solution has a higher solute potential?
- At equilibrium which chamber will have lower water potential?
- If one chamber has a of - 2000 kPa, and the other - 1000 kPa, which is the chamber that has the higher?
- What will be the direction of the movement of water when two solutions with $= 0.2 \text{ MPa}$ and $= 0.1 \text{ MPa}$ are separated by a selectively permeable membrane?

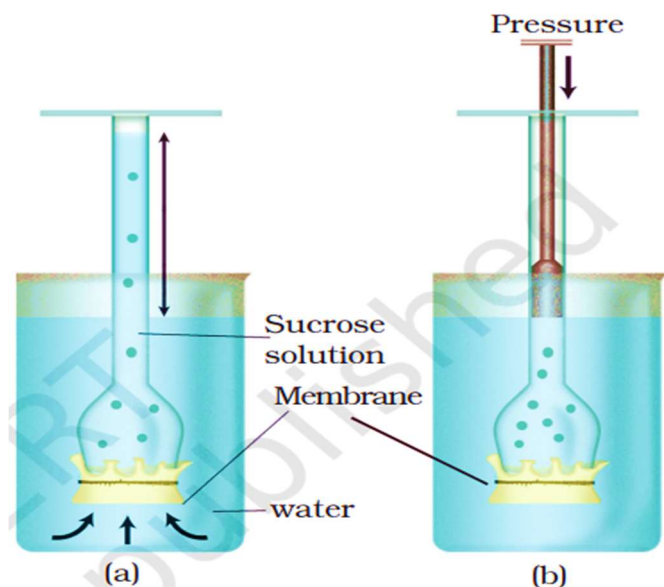


Figure 21: Osmosis experiments: Numerically osmotic pressure is equivalent to the osmotic potential, but the sign is opposite

Let us discuss another experiment where a solution of sucrose in water taken in a funnel is separated from pure water in a beaker by a selectively permeable membrane (Figure 11.4). You can get this kind of a membrane in an egg. Remove the yolk and albumin through a small hole at one end of the egg, and place the shell in dilute solution of hydrochloric acid for a

few hours. The egg shell dissolves leaving the membrane intact. Water will move into the funnel, resulting in rise in the level of the solution in the funnel. This will continue till the equilibrium is reached. In case sucrose does diffuse out through the membrane, will this equilibrium be ever reached?

External pressure can be applied from the upper part of the funnel such that no water diffuses into the funnel through the membrane. This pressure required to prevent water from diffusing is in fact, the osmotic pressure and this is the function of the solute concentration; more the solute concentration, greater will be the pressure required to prevent water from diffusing in. Numerically osmotic pressure is equivalent to the osmotic potential, but the sign is opposite. Osmotic pressure is the positive pressure applied, while osmotic potential is negative.

11.2.3 Plasmolysis

The behaviour of the plant cells (or tissues) with regard to water movement depends on the surrounding solution. If the external solution balances the osmotic pressure of the cytoplasm, it is said to be isotonic. If the external solution is more dilute than the cytoplasm, it is hypotonic and if the external solution is more concentrated, it is hypertonic. Cells swell in hypotonic solutions and shrink in hypertonic ones.

Plasmolysis occurs when water moves out of the cell and the cell membrane of a plant cell shrinks away from its cell wall. This occurs when the cell (or tissue) is placed in a solution that is hypertonic (has more solutes) to the protoplasm. Water moves out; it is first lost from the cytoplasm and then from the vacuole. The water when drawn out of the cell through diffusion into the extracellular (outside cell) fluid causes the protoplast to shrink away from the walls. The cell is said to be plasmolyzed. The movement of water occurred across the membrane moving from an area of high-water potential (i.e., the cell) to an area of lower water potential outside the cell.

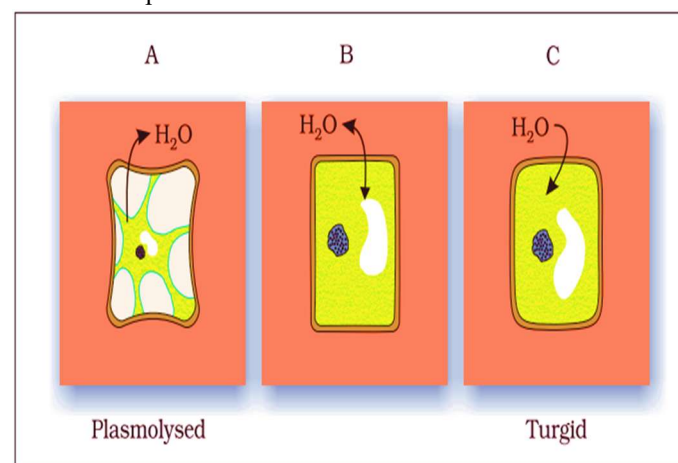


Figure 22: Plasmolyzed and turgid cells

What occupies the space between the cell wall and the shrunken protoplast in the plasmolyzed cell?

When the cell (or tissue) is placed in an isotonic solution, there is no net flow of water towards the inside or outside. If the

external solution balances the osmotic pressure of the cytoplasm it is said to be isotonic. When water flows into the cell and out of the cell and are in equilibrium, the cells are said to be flaccid.

The process of plasmolysis is usually reversible. When the cells are placed in a hypotonic solution (higher water potential or dilute solution as compared to the cytoplasm), water diffuses into the cell causing the cytoplasm to build up a pressure against the wall, that is called turgor pressure. The pressure exerted by the protoplasts due to entry of water against the rigid walls is called pressure potential Ψ_p . Because of the rigidity of the cell wall, the cell does not rupture. This turgor pressure is ultimately responsible for enlargement and extension growth of cells.

What would be the Ψ_p of a flaccid cell? Which organisms other than plants possess cell wall?

11.2.4. Imbibition

Imbibition is a special type of diffusion when water is absorbed by solids - colloids - causing them to increase in volume. The classical examples of imbibition are absorption of water by seeds and dry wood. The pressure that is produced by the swelling of wood had been used by prehistoric man to split rocks and boulders. If it were not for the pressure due to imbibition, seedlings would not have been able to emerge out of the soil into the open; they probably would not have been able to establish!

Imbibition is also diffusion since water movement is along a concentration gradient; the seeds and other such materials have almost no water hence they absorb water easily. Water potential gradient between the absorbent and the liquid imbibed is essential for imbibition. In addition, for any substance to imbibe any liquid, affinity between the adsorbant and the liquid is also a pre-requisite.

11.3. LONG DISTANCE TRANSPORT OF WATER

At some earlier stage you might have carried out an experiment where you had placed a twig bearing white flowers in coloured water and had watched it turn colour. On examining the cut end of the twig after a few hours you had noted the region through which the coloured water moved. That experiment very easily demonstrates that the path of water movement is through the vascular bundles, more specifically, the xylem. Now we have to go further and try and understand the mechanism of movement of water and other substances up a plant.

Long distance transport of substances within a plant cannot be by diffusion alone. Diffusion is a slow process. It can account for only short distance movement of molecules. For example, the movement of a molecule across a typical plant cell (about 50 μm) takes approximately 2.5 s. At this rate, can you calculate how many years it would take for the movement of molecules over a distance of 1 m within a plant by diffusion alone? In large and complex organisms, often substances have to be moved to long distances. Sometimes the sites of production or absorption and sites of storage are too far from each other; diffusion or

active transport would not suffice. Special long-distance transport systems become necessary so as to move substances across long distances and at a much faster rate. Water and minerals, and food are generally moved by a mass or bulk flow system.

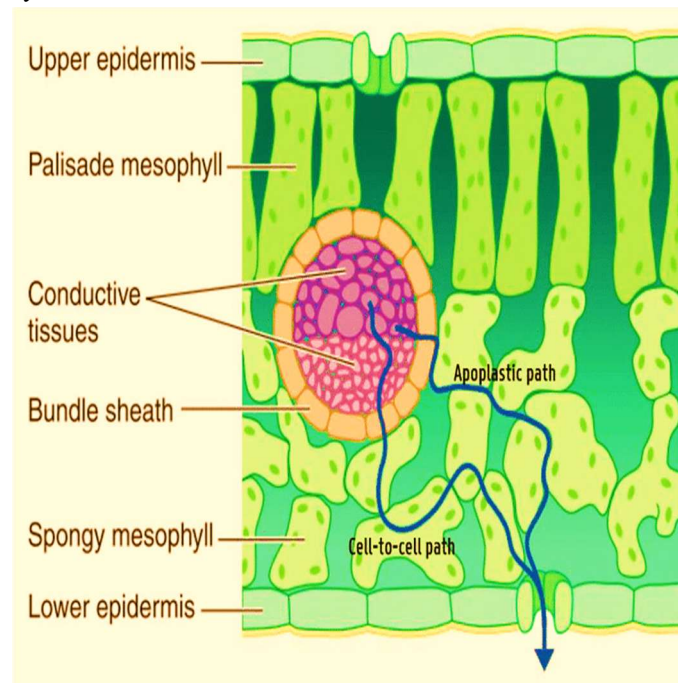


Figure 23: Long distance transport of water

Mass flow is the movement of substances in bulk or in masse from one point to another as a result of pressure differences between the two points. It is a characteristic of mass flow that substances, whether in solution or in suspension, are swept along at the same pace, as in a flowing river. This is unlike diffusion where different substances move independently depending on their concentration gradients. Bulk flow can be achieved either through a positive hydrostatic pressure gradient (e.g., a garden hose) or a negative hydrostatic pressure gradient (e.g., suction through a straw).

The bulk movement of substances through the conducting or vascular tissues of plants is called translocation. Do you remember studying cross sections of roots, stems and leaves of higher plants and studying the vascular system? The higher plants have highly specialised vascular tissues - xylem and phloem. Xylem is associated with translocation of mainly water, mineral salts, some organic nitrogen and hormones, from roots to the aerial parts of the plants. The phloem translocates a variety of organic and inorganic solutes, mainly from the leaves to other parts of the plants.

11.4. How do Plants Absorb Water?

We know that the roots absorb most of the water that goes into plants; obviously that is why we apply water to the soil and not on the leaves. The responsibility of absorption of water and minerals is more specifically the function of the root hairs that are present in millions at the tips of the roots. Root hairs are

thin-walled slender extensions of root epidermal cells that greatly increase the surface area for absorption. Water is absorbed along with mineral solutes, by the root hairs, purely by diffusion. Once water is absorbed by the root hairs, it can move deeper into root layers by two distinct pathways:

(1.) apoplast pathway (2.) symplast pathway

The apoplast is the system of adjacent cell walls that is continuous throughout the plant, except at the Casparian strips of the endodermis in the roots. The apoplastic movement of

water occurs exclusively through the intercellular spaces and the walls of the cells. Movement through the apoplast does not involve crossing the cell membrane. This movement is dependent on the gradient. The apoplast does not provide any barrier to water movement and water movement is through mass flow. As water evaporates into the intercellular spaces or the atmosphere, tension develop in the continuous stream of water in the apoplast, hence mass flow of water occurs due to the adhesive and cohesive properties of water.

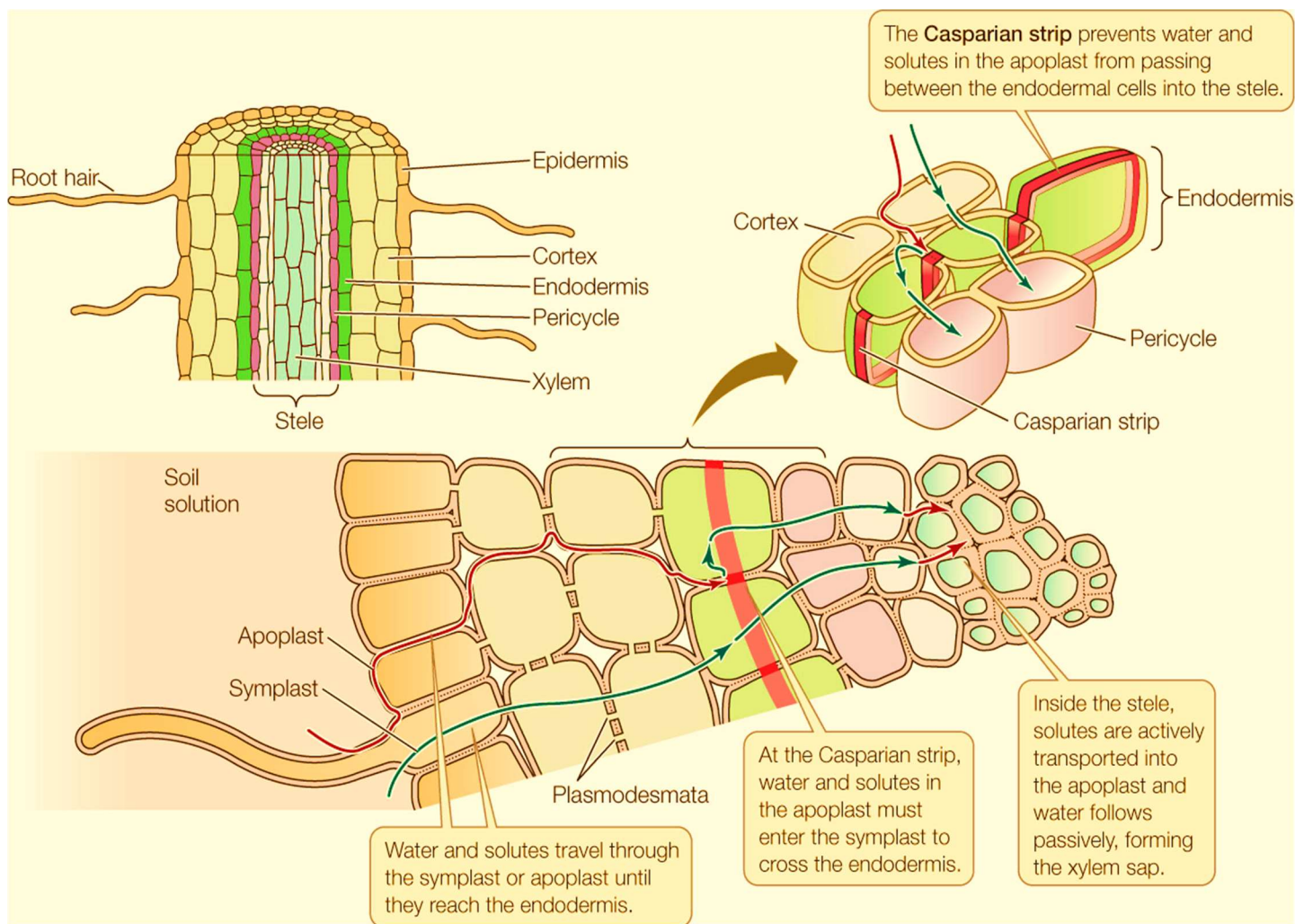


Figure 24: Water absorption in plants is a complex and finely regulated process crucial for their survival and optimal growth. This multifaceted journey of water from the soil to the various plant tissues involves several distinct pathways. Each of these pathways, known as the symplast, apoplast, and transmembrane pathways, plays a significant role in facilitating the movement of water through plant roots and ultimately into the entire plant system. Source: <https://www.preachbio.com/2024/01/hydrological-dynamics-unraveling.html>

The symplastic system is the system of interconnected protoplasts. Neighboring cells are connected through cytoplasmic strands that extend through plasmodesmata. During symplastic movement, the water travels through the cells - their cytoplasm; intercellular movement is through the plasmodesmata. Water has to enter the cells through the cell membrane, hence the movement is relatively slower. Movement is again down a potential gradient. Symplastic

movement may be aided by cytoplasmic streaming. You may have observed cytoplasmic streaming in cells of the Hydrilla leaf; the movement of chloroplast due to streaming is easily visible. Most of the water flow in the roots occurs via the apoplast since the cortical cells are loosely packed, and hence offer no resistance to water movement. However, the inner boundary of the cortex, the endodermis, is impervious to water

because of a band of suberized matrix called the Casparian strip. Water molecules are unable to penetrate the layer, so they are

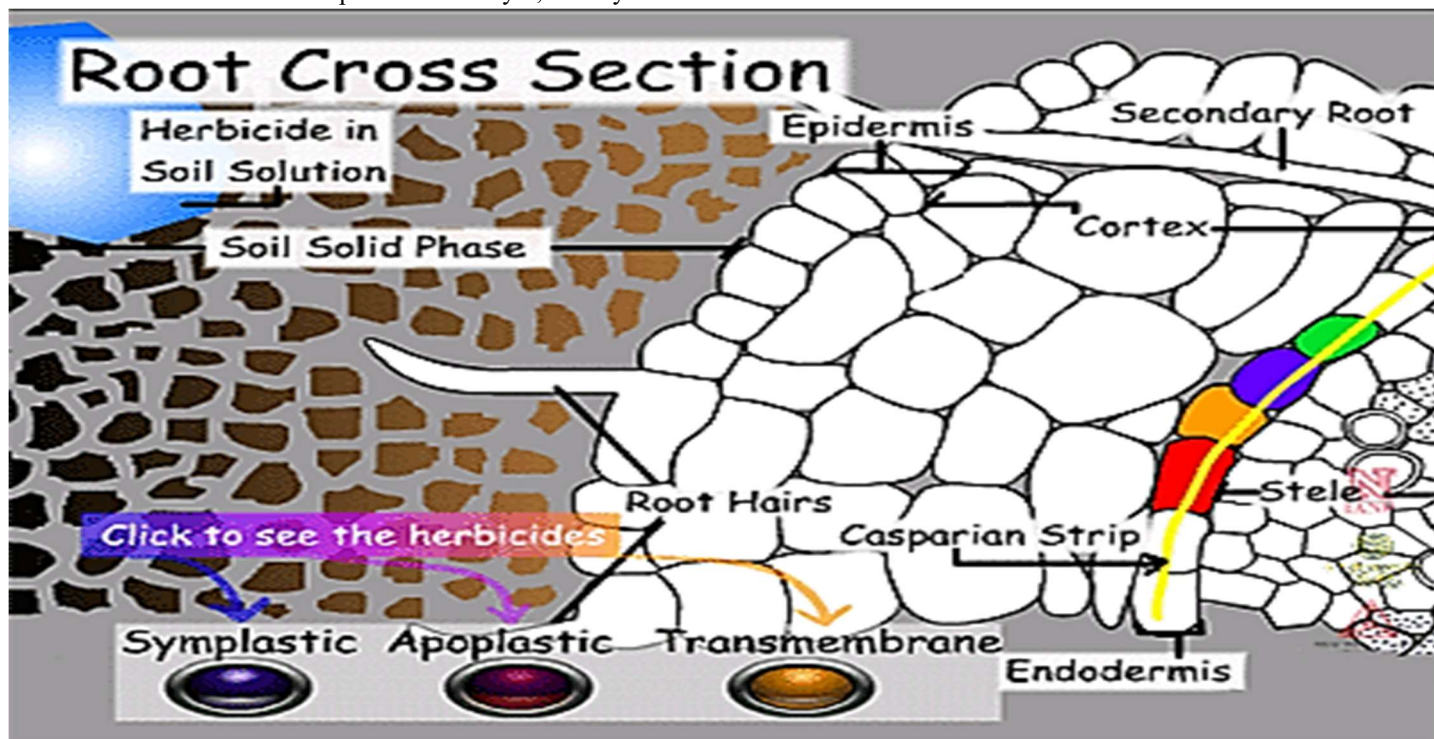


Figure 25: Pathways for Root Absorption

directed to wall regions that are not suberized, into the cells proper through the membranes.

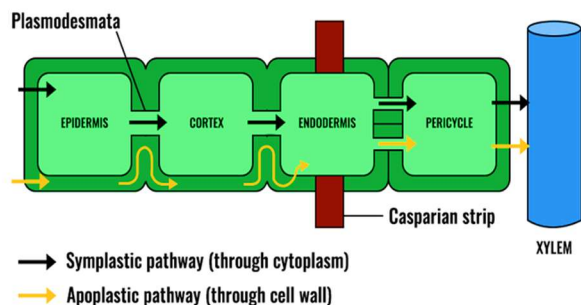


Figure 26: The views of Symplast v/s apoplast

The water then moves through the symplast and again crosses a membrane to reach the cells of the xylem. The movement of water through the root layers is ultimately symplastic in the endodermis. This is the only way water and other solutes can enter the vascular cylinder. Once inside the xylem, water is again free to move between cells as well as through them. In young roots, water enters directly into the xylem vessels and/or tracheid's. These are non-living conduits and so are parts of the apoplast. The path of water and mineral ions into the root vascular system is summarized in Figure. Some plants have additional structures associated with them path Pericycle that help in water (and mineral) absorption. A mycorrhiza is a symbiotic association of a fungus with a root system. The

fungus filaments form a network around the young root or they penetrate the root cells.

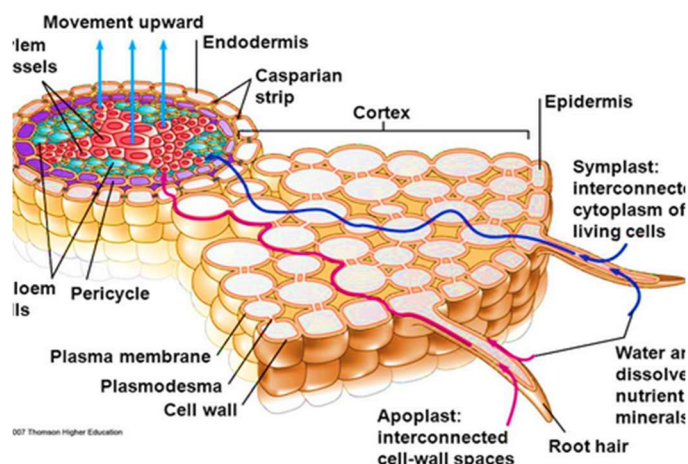


Figure 27: Symplast and Apoplast Pathways in Plants

The hyphae have a very large surface area that absorb mineral ions and water from the soil from a much larger volume of soil that perhaps a root cannot do. The fungus provides minerals and water to the roots, in turn the roots provide sugars and N-containing compounds to the mycorrhizae. Some plants have an obligate association with the mycorrhizae. For example, Pinus seeds cannot germinate and establish without the presence of mycorrhizae.

11.4. Water Movement up a Plant

We looked at how plants absorb water from the soil, and move it into the vascular tissues. We now have to try and understand

how this water is transported to various parts of the plant. Is the water movement active, or is it still passive? Since the water has to be moved up a stem against gravity, what provides the energy for this?

11.4.1. Root Pressure

As various ions from the soil are actively transported into the vascular tissues of the roots, water follows (its potential gradient) and increases the pressure inside the xylem. This positive pressure is called root pressure, and can be responsible for pushing up water to small heights in the stem. How can we see that root pressure exists? Choose a small soft-stemmed plant and on a day, when there is plenty of atmospheric moisture, cut the stem horizontally near the base with a sharp blade, early in the morning. You will soon see drops of solution ooze out of the cut stem; this comes out due to the positive root pressure. If you fix a rubber tube to the cut stem as a sleeve you can actually collect and measure the rate of exudation, and also determine the composition of the exudates. Effects of root pressure is also observable at night and early morning when evaporation is low, and excess water collects in the form of droplets around special openings of veins near the tip of grass blades, and leaves of many herbaceous parts. Such water loss in its liquid phase is known as guttation.

Root pressure can, at best, only provide a modest push in the overall process of water transport. They obviously do not play a major role in water movement up tall trees. The greatest contribution of root pressure may be to re-establish the continuous chains of water molecules in the xylem which often break under the enormous tensions created by transpiration. Root pressure does not account for the majority of water transport; most plants meet their need by respiratory pull.

11.4.2. Transpiration pulls

Despite the absence of a heart or a circulatory system in plants, the upward flow of water through the xylem in plants can achieve fairly high rates, up to 15 meters per hour. How is this movement accomplished? A long-standing question is, whether water is 'pushed' or 'pulled' through the plant. Most researchers agree that water is mainly 'pulled' through the plant, and that the driving force for this process is transpiration from the leaves. This is referred to as the cohesion-tension-transpiration pull model of water transport. But, what generates this transpirational pull?

Water is transient in plants. Less than 1 per cent of the water reaching the leaves is used in photosynthesis and plant growth. Most of it is lost through the stomata in the leaves. This water loss is known as transpiration.

You have studied transpiration in an earlier class by enclosing a healthy plant in polythene bag and observing the droplets of water formed inside the bag. You could also study water loss from a leaf using cobalt chloride paper, which turns colour on absorbing water.

11.4.3. TRANSPIRATION

Transpiration is the evaporative loss of water by plants. It occurs mainly through stomata (sing.: stoma). Besides the loss of water vapours in transpiration, exchange of oxygen and carbon dioxide in the leaf also occurs through these stomata. Normally stomata are open in the day time and close during the night. The immediate cause of the opening or closing of stomata is a change in the turgidity of the guard cells. The inner wall of each guard cell, towards the pore or stomatal aperture, is thick and elastic. When turgidity increases within the two guard cells flanking each stomatal aperture or pore, the thin outer walls bulge out and force the inner walls into a crescent shape. The opening of the stoma is also aided due to the orientation of the microfibrils in the cell walls of the guard cells. Cellulose microfibrils are oriented radially rather than longitudinally making it easier for the stoma to open. When the guard cells lose turgor, due to water loss (or water stress) the elastic inner walls regain their original shape, the guard cells become flaccid and the stoma closes.

Usually the lower surface of a dorsiventral (often dicotyledonous) leaf has a greater number of stomata while in an isobilateral (often monocotyledonous) leaf they are about equal on both surfaces. Transpiration is affected by several external factors: temperature, light, humidity, wind speed. Plant factors that affect transpiration include number and distribution of stomata, per cent of open stomata, water status of the plant, canopy structure etc.

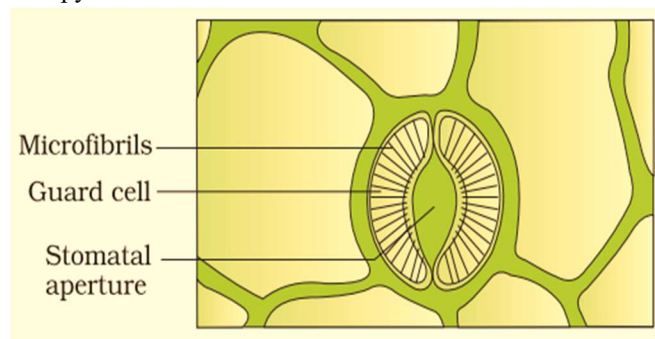


Figure 28: Morphology of Stomatal aperture

The transpiration driven ascent of xylem sap depends mainly on the following physical properties of water:

- Cohesion - mutual attraction between water molecules.
- Adhesion - attraction of water molecules to polar surfaces (such as the surface of tracheary elements).
- Surface Tension - water molecules are attracted to each other in the liquid phase more than to water in the gas phase.

These properties give water high tensile strength, i.e., an ability to resist a pulling force, and high capillarity, i.e., the ability to rise in thin tubes. In plants capillarity is aided by the small diameter of the tracheary elements - the tracheid's and vessel elements.

The process of photosynthesis requires water. The system of xylem vessels from the root to the leaf vein can supply the

needed water. But what force does a plant use to move water molecules into the leaf parenchyma cells where they are needed? As water evaporates through the stomata, since the thin film of water over the cells is continuous, it results in pulling of water, molecule by molecule, into the leaf from the xylem. Also, because of the lower concentration of water vapour in the atmosphere as compared to the substomatal cavity and intercellular spaces, water diffuses into the surrounding air. This creates a 'pull' (Figure 11.9). Measurements reveal that the forces generated by transpiration can create pressures sufficient to lift a xylem-sized column of water over 130 meters high.

11.5. Transpiration and Photosynthesis - a Compromise

Transpiration has more than one purpose; it

- Creates transpiration pull for absorption and transport of water in plants
- Supplies water for photosynthesis
- Transports minerals from the soil to all parts of the plant
- Cools leaf surfaces, sometimes 10 to 15 degrees, by evaporative cooling
- Maintains the shape and structure of the plants by keeping cells turgid

An actively photosynthesizing plant has an insatiable need for water. Photosynthesis is limited by available water which can be swiftly depleted by transpiration. The humidity of rainforests is largely due to this vast cycling of water from root to leaf to atmosphere and back to the soil.

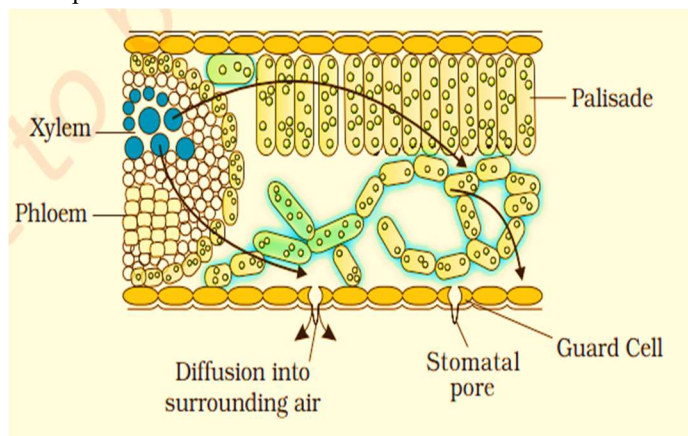


Figure 29: Stomatal activity with movements of water

The evolution of the C4 photosynthetic system is probably one of the strategies for maximizing the availability of CO₂ while minimizing water loss. C4 plants are twice as efficient as C3 plants in terms of fixing carbon dioxide (making sugar). However, a C4 plant loses only half as much water as a C3 plant for the same amount of CO₂ fixed.

11.6. UPTAKE AND TRANSPORT OF MINERAL NUTRIENTS

Plants obtain their carbon and most of their oxygen from CO₂ in the atmosphere. However, their remaining nutritional requirements are obtained from water and minerals in the soil.

11.6.1 Uptake of Mineral Ions

Unlike water, all minerals cannot be passively absorbed by the roots. Two factors account for this: (i) minerals are present in the soil as charged particles (ions) which cannot move across cell membranes and (ii) the concentration of minerals in the soil is usually lower than the concentration of minerals in the root. Therefore, most minerals must enter the root by active absorption into the cytoplasm of epidermal cells. This needs energy in the form of ATP. The active uptake of ions is partly responsible for the water potential gradient in roots, and therefore for the uptake of water by osmosis. Some ions also move into the epidermal cells passively.

Ions are absorbed from the soil by both passive and active transport. Specific proteins in the membranes of root hair cells actively pump ions from the soil into the cytoplasm of the epidermal cells. Like all cells, the endodermal cells have many transport proteins embedded in their plasma membrane; they let some solutes cross the membrane, but not others. Transport proteins of endodermal cells are control points where a plant adjusts the quantity and types of solutes that reach the xylem. Note that the root endodermis, because of the layer of suberin, has the ability to actively transport ions in one direction only.

11.6.2 Translocation of Mineral Ions

After the ions have reached xylem through active or passive uptake, or a combination of the two, their further transport up the stem to all parts of the plant is through the transpiration stream. The chief sinks for the mineral elements are the growing regions of the plant, such as the apical and lateral meristems, young leaves, developing flowers, fruits and seeds, and the storage organs. Unloading of mineral ions occurs at the fine vein endings through diffusion and active uptake by these cells. Mineral ions are frequently remobilized, particularly from older, senescing parts. Older dying leaves export much of their mineral content to younger leaves. Similarly, before leaf fall in deciduous plants, minerals are removed to other parts. Elements most readily mobilized are phosphorus, Sulphur, nitrogen and potassium. Some elements that are structural components like calcium are not remobilized. An analysis of the xylem exudates shows that though some of the nitrogen travels as inorganic ions, much of it is carried in the organic form as amino acids and related compounds. Similarly, small amounts of P and S are carried as organic compounds. In addition, small amount of exchange of materials does take place between xylem and phloem. Hence, it is not that we can clearly make a distinction and say categorically that xylem transports only inorganic nutrients while phloem transports only organic materials, as was traditionally believed.

11.7. PHLOEM TRANSPORT: FLOW FROM SOURCE TO SINK

Food, primarily sucrose, is transported by the vascular tissue phloem from a source to a sink. Usually the source is understood to be that part of the plant which synthesizes the

food, i.e., the leaf, and sink, the part that needs or stores the food. But, the source and sink may be reversed depending on the season, or the plant's needs. Sugar stored in roots may be mobilized to become a source of food in the early spring when the buds of trees, act as sink; they need energy for growth and development of the photosynthetic apparatus. Since the source-sink relationship is variable, the direction of movement in the phloem can be upwards or downwards, i.e., bi-directional. This contrasts with that of the xylem where the movement is always unidirectional, i.e., upwards. Hence, unlike one-way flow of water in transpiration, food in phloem sap can be transported in any required direction so long as there is a source of sugar and a sink able to use, store or remove the sugar.

Phloem sap is mainly water and sucrose, but other sugars, hormones and amino acids are also transported or translocated through phloem.

11.8. The Pressure Flow or Mass Flow Hypothesis

The accepted mechanism used for the translocation of sugars from source to sink is called the pressure flow hypothesis. (see Figure 11.10). As glucose is prepared at the source (by photosynthesis) it is converted to sucrose (a disaccharide). The sugar is then moved in the form of sucrose into the companion cells and then into the living phloem sieve tube cells by active transport. This process of loading at the source produces a hypertonic condition in the phloem. Water in the adjacent xylem moves into the phloem by osmosis. As osmotic pressure builds up the phloem sap will move to areas of lower pressure. At the sink osmotic pressure must be reduced. Again, active transport is necessary to move the sucrose out of the phloem sap and into the cells which will use the sugar - converting it into energy, starch, or cellulose. As sugars are removed, the osmotic pressure decreases and water moves out of the phloem.

To summarize, the movement of sugars in the phloem begins at the source, where sugars are loaded (actively transported) into a sieve tube. Loading of the phloem sets up a water potential gradient that facilitates the mass movement in the phloem.

Phloem tissue is composed of sieve tube cells, which form long columns with holes in their end walls called sieve plates. Cytoplasmic strands pass through the holes in the sieve plates, so forming continuous filaments. As hydrostatic pressure in the sieve tube of phloem increases, pressure flow begins, and the sap moves through the phloem. Meanwhile, at the sink, incoming sugars are actively transported out of the phloem and removed as complex carbohydrates. The loss of solute produces a high-water potential in the phloem, and water passes out, returning eventually to the xylem. A simple experiment, called girdling, was used to identify the tissues through which food is transported. On the trunk of a tree, a ring of bark up to the depth of the phloem layer can be carefully removed. In the absence of downward movement of food, the portion of the bark above the ring on the stem becomes swollen after a few weeks. This simple experiment shows that phloem is the tissue responsible

for translocation of food, and that transport takes place in one direction, i.e., towards the roots. This experiment can be performed by you easily.

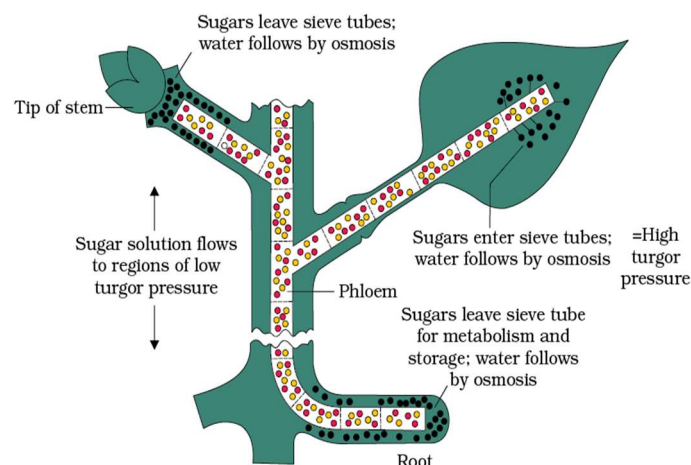


Figure 26: Synthesized the sugar in plants

12. Summary

Plants obtain a variety of inorganic elements (ions) and salts from their surroundings especially from water and soil. The movement of these nutrients from environment into the plant as well as from one plant cell to another plant cell essentially involves movement across a cell membrane. Transport across cell membrane can be through diffusion, facilitated transport or active transport. Water and minerals absorbed by roots are transported by xylem and the organic material synthesized in the leaves is transported to other parts of plant through phloem. Passive transport (diffusion, osmosis) and active transport are the two modes of nutrient transport across cell membranes in living organisms. In passive transport, nutrients move across the membrane by diffusion, without any use of energy as it is always down the concentration gradient and hence entropy driven. This diffusion of substances depends on their size, solubility in water or organic solvents. Osmosis is the special type of diffusion of water across a selectively permeable membrane which depends on pressure gradient and concentration gradient. In active transport, energy in the form of ATP is utilised to pump molecules against a concentration gradient across membranes. Water potential is the potential energy of water molecules which helps in the movement of water. It is determined by solute potential and pressure potential. The osmotic behaviour of cells depends on the surrounding solution. If the surrounding solution of the cell is hypertonic, it gets plasmolyzed. The absorption of water by seeds and dry wood takes place by a special type of diffusion called imbibition. In higher plants, there is a vascular system comprising xylem and phloem, responsible for translocation. Water, minerals and food cannot be moved within the body of a plant by diffusion alone. They are therefore transported by a mass flow system - movement of substance in bulk from one point to another as a result of pressure differences between the

two points. Water absorbed by root hairs moves into the root tissue by two distinct pathways, i.e., apoplast and symplast. Various ions and water from soil can be transported up to a small height in stems by root pressure. The transpiration pull model is the most acceptable to explain the transport of water. Transpiration is the loss of water in the form of vapour from the plant parts through stomata. Temperature, light, humidity, wind speed and number of stomata affect the rate of transpiration. Excess water is also removed through the tips of leaves of plants by guttation.

13. Ethics declarations

13.1. Ethics approval and consent to participate

Not applicable.

13.2. Consent for publication

Not applicable.

13.3. Competing interests

The authors declare that they have no competing interests.

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22. Background: The integration of Artificial Intelligence (AI) in agricultural practices has witnessed substantial advancements, with a focus on enhancing efficiency and sustainability. This research explores the application of AI-powered robotic harvesting systems for legume crops, aiming to revolutionize traditional harvesting methods. By leveraging machine learning algorithms and robotic technology, this study investigates the feasibility and performance of such systems in terms of precision, speed, and resource optimization

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