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Soil to Stem: The Journey of Nutrients in Plant Growth

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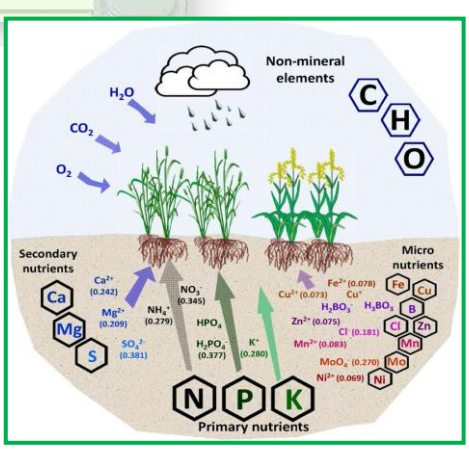
The movement of nutrients in soil and their subsequent absorption by plants is a critical process for plant growth and development. Nutrients, which are chemical compounds required for growth and metabolism, are taken up by plants through various metabolic processes. According to Arnon and Stout's (1939) essentiality criteria, for a nutrient to be considered essential, it must be required for a plant to complete its life cycle, and its deficiency should specifically impact the plant's metabolism. Essential nutrients include basic elements like carbon, hydrogen, and oxygen, primary elements such as nitrogen, phosphorus, and potassium, and micronutrients like zinc and iron. Nutrient movement from soil to plant roots occurs via three primary mechanisms: mass flow, diffusion, and root interception. Mass flow refers to the movement of nutrients with water toward plant roots during transpiration, while diffusion allows nutrients to move from areas of higher concentration in the soil solution to lower concentration at the root surface. Root interception occurs when roots physically come into contact with nutrient-rich soil particles, facilitating nutrient uptake. Once inside the plant root, nutrient ions are absorbed through both passive and active transport mechanisms. Passive transport moves ions along concentration gradients without energy expenditure, while active transport requires energy to move ions against concentration gradients. Various theories, including the carbonic acid exchange theory and Donnan's equilibrium theory, explain the mechanisms of nutrient uptake and ion exchange in plants. Understanding the movement and absorption of nutrients is essential for optimizing soil management and enhancing plant nutrient use efficiency, which is vital for improving crop productivity and sustainability in agricultural systems.

Keywords: Plant nutrition, nutrient absorption, essential elements, mass flow, diffusion, root interception, active transport, passive transport, ion uptake

Introduction

Plant nutrition involves the supply and absorption of essential chemical compounds necessary for growth and metabolism. These compounds, referred to as nutrients, are vital for various metabolic processes within the plant. Metabolism encompasses all the biochemical reactions in living cells that convert nutrients into cellular material, energy, or metabolic intermediates, ensuring the maintenance of life and growth (Taiz and Zeiger, 2010). Therefore, nutrition and metabolism are inherently connected, as nutrients fuel the biochemical pathways that sustain plant functions (Marschner,



2012). Higher plants rely primarily on inorganic nutrients, including macronutrients such as nitrogen (N), phosphorus (P), and potassium (K), as well as micronutrients like iron (Fe) and zinc (Zn), to support their physiological processes (Kramer and Johnson, 2018). Nitrogen is crucial for the synthesis of amino acids, proteins, and nucleic acids, while phosphorus plays a vital role in energy transfer and photosynthesis (Raghothama, 1999). Potassium regulates various physiological functions, including osmoregulation and enzyme activation (Marschner, 2012). The balance and availability of these essential nutrients significantly influence plant health, development, and productivity (Fageria *et al.*, 2009). Understanding the intricate relationship between nutrient availability and metabolic processes is essential for optimizing plant growth and enhancing agricultural productivity.

Essentiality criteria

According to **Arnon and Stout (1939)**, for an element to be considered an essential plant nutrient, three criteria must be met,

1. A deficiency of an element makes it impossible for the plant to complete its life cycle.
2. The deficiency is specific to the element in question.
3. The element is directly involved in the nutrition of the plant, for example as a constituent of an essential metabolite or required for the action of an enzyme system.

Essential elements

Arnon and Stout (1939) proposed the following chemical elements are essential for higher plants,

- Basic elements - Carbon (C), Hydrogen (H), Oxygen (O)
- Primary elements - Nitrogen (N), Phosphorous (P), Potassium (K)
- Secondary elements - Calcium (C), Magnesium (M), Sulphur (S)
- Micronutrients - Iron (Fe), Zinc (Zn), Copper (Cu), Manganese (Mn), Boron (B), Molybdenum (Mo), Chlorine (Cl), Nickel (Ni).

Movement of nutrients from soil to root surface

There are three basic mechanisms (Figure 1) through which nutrients and salts come in contact with plant roots. They are (1) mass flow (2) diffusion and (3) root interception.

1. **Mass flow** – the movement of the nutrients with water.
2. **Diffusion** - movement through water in response to a concentration gradient.
3. **Root interception** - growing roots move into the soil and displace it. In the process, roots come in contact with the soil and intercept the nutrients from the soil through contact exchange.

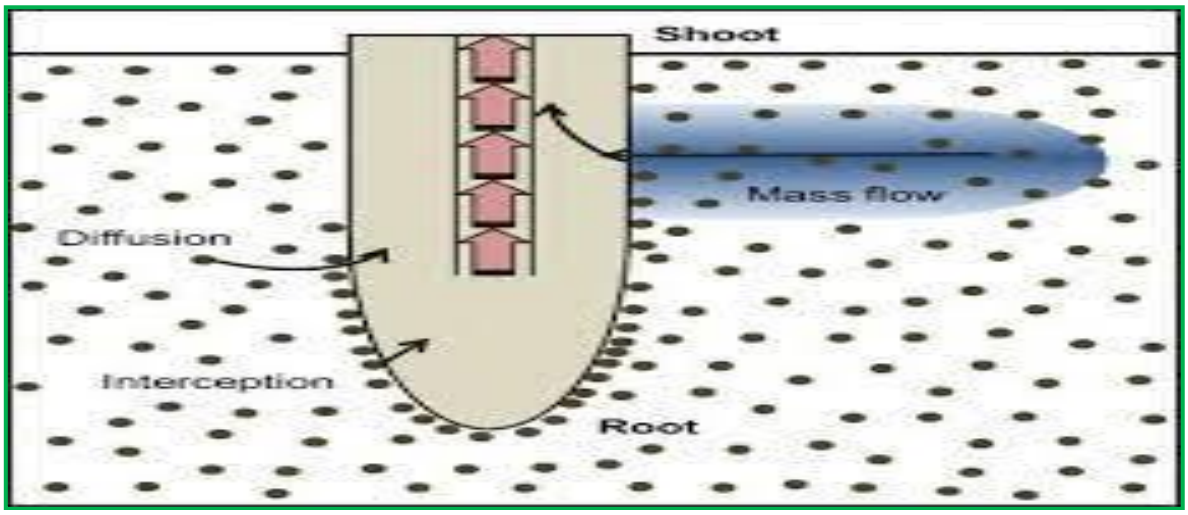


Figure 1: Nutrient movement from soil to the root surface

1. **Mass flow:**

- Mass flow occurs when nutrients are transported to the surface of roots by the movement of water in the soil (*i.e.*, percolation, transpiration, or evaporation).
- Mass flow is the movement of dissolved nutrients into a plant as the plant absorbs water for transpiration.
- As plants transpire water, water moves from the bulk to the roots by mass or convective flow.
- The rate of water flow governs the amount of nutrients that are transported to the root surface. Therefore, mass flow decreases as soil water decreases.
- The rate of nutrient transport by mass flow (J) is given by the rate of water flux into the root (v) and the concentration of the ion in solution (Ci) *i.e.*, **J = V x Ci**
- Most of the **nitrogen, calcium, magnesium, sulfur, copper, boron, manganese and molybdenum** move to the root by mass flow.

2. **Diffusion:**

- Diffusion is the movement of a particular nutrient along a concentration gradient.
- The movement of nutrients to the root surface in response to a concentration gradient.
- When there is a difference in concentration of a particular nutrient within the soil solution, the nutrient will move from an area of higher concentration to an area of lower concentration.
- When nutrients are found in higher concentrations in one area than another, there is a net movement to the low-concentration area so that equilibrium is reached.
- Thus, a high concentration in the soil solution and a low concentration at the root cause the nutrients to move to the root surface, where they can be taken up.
- You may have observed the phenomenon of diffusion when adding sugar to water. As the sugar dissolves, it moves through parts of the water with lower sugar concentration until it is evenly distributed, or uniformly concentrated. Diffusion delivers appreciable amounts of **phosphorus, potassium, zinc, and iron** to the root surface. Diffusion is a relatively slow process compared to the mass flow of nutrients with water movement toward the root.
- When mass flow is unable to supply sufficient quantities of a nutrient and a continued uptake occurs, the concentration of the nutrient at the root surface is reduced and a concentration gradient is established.
- Ions move by thermal motion from points of higher concentration to those of lower concentration when a concentration gradient exists.
- The movement of nutrient ions in response to the concentration gradient is termed diffusion.
- The amount of a nutrient ion diffusing across a unit area in unit time (F) with a concentration gradient (dC/dx) can be explained with the help of Steady-state diffusion by **Fick's First Law of diffusion** *i.e.*, **F = -D. (dC/dx)**
- The equation applies to a linear gradient with a minus sign indicating the movement is occurring from a higher concentration to a lower one.
- The rate of diffusion depends on the concentration gradient and several factors that influence the diffusion coefficient. Diffusion coefficients for ions in water are similar, but in soil, they differ significantly due to interactions between ions and the soil matrix.
- Nearly the entire amount of K is provided by diffusion, followed by P.

3. **Root interception:**

- The term root interception was coined by **Stanley A Barber** of Purdue State University, USA.
- Root interception occurs when a nutrient comes into physical contact with the root surface.

- The root interception increases as the root surface area and mass increase, thus enabling the plant to explore a greater amount of soil.
- Root interception may be enhanced by mycorrhizal fungi, which colonize roots and increase root exploration into the soil.
- Root interception is responsible for an appreciable amount of calcium uptake, and some amounts of magnesium, zinc and manganese.
- Root interception occurs when the growth of a root causes contact with soil colloids which contain nutrients. The root then absorbs the nutrients. It is an important mode of transport for **calcium and magnesium**, but in general is a minor pathway for nutrient transfer.

Water moves into the root through osmosis and capillary action

- Soil water contains dissolved particles, such as plant nutrients. These dissolved particles within soil water are referred to as **solutes**.
- **Osmosis** is the movement of soil water from areas of low solute concentration to areas of high solute concentration. Osmosis is essentially the diffusion of soil water.
- **Capillary action** results from water's adhesive (attraction to solid surfaces) and cohesion (attraction to other water molecules). Capillary action enables water to move upwards, against the force of gravity, into the plant water from the surrounding soil.

Nutrient ions move into the plant root by

1. **Diffusion -** the movement of ions along a high-to-low concentration gradient.
2. **Ion exchange** - Cation ion exchange occurs when nutrient cations are attracted to the charged surface of cells within the root, called cortex cells. When cation exchange occurs, the plant root releases a hydrogen ion. Thus, cation exchange in the root causes the pH of the immediately surrounding soil to decrease.

Once water and nutrient ions enter the plant root, they move through spaces that exist within the root tissue between neighboring cells. Water and nutrients are then transported into the xylem, which conducts water and nutrients to all parts of the plant. Once water and nutrients enter the xylem, both can be transported to other parts in the plant where the water and nutrients are needed. The basic outline of how nutrient ions are absorbed by plant cells follows.

Absorption of nutrients into plant cells

Plant cells contain barriers like plasma membrane and tonoplast that selectively regulate the movement of water and nutrients into and out of the cell.These cell barriers are;

- Permeable to oxygen, carbon dioxide, as well as certain compounds.
- Semi-permeable to water.
- Selectively permeable to inorganic ions and organic compounds, such as amino acids and sugars.

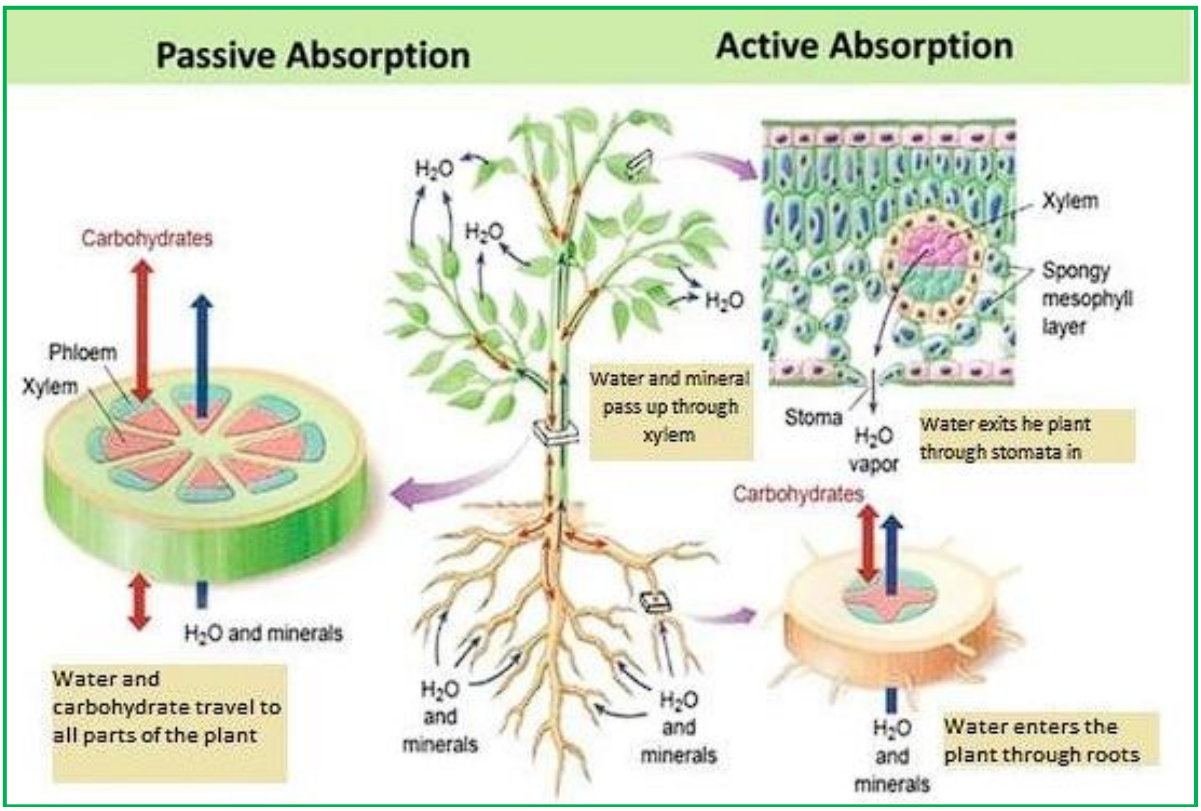
Nutrient ions move across barriers in two ways:

Nutrient ions may move across these barriers passively or actively.

1. **Passive transport or absorption:**

- Absorption of ions by plant roots along the electro-chemical potential gradient.
- Passive transport is the diffusion of an ion along a concentration gradient.
- When the interior of the cell has a lower concentration of a specific nutrient than the outside of the cell, the nutrient can diffuse into the cell
- For this process there is no consumption of metabolic energy (the nutrients enter with water). Thus, it occurs in dead or non respiring tissues.
- The process is non sensitive to inhibitors and there is no ion selectivity (no specificity).

- Extracellular spaces exist in the mesophyll cells of leaves where ions are able to diffuse and exchange.
- Most of the nutrient ions reach the "outer" space of the leaves via the xylem, from the roots.
- Mineral ions in rains, irrigation water and in foliar applications penetrate leaves through the stomata and cuticle to reach the interior of leaves where they become available for absorption by mesophyll cells.



2. Active transport or absorption:

- Active transport is the movement of a nutrient ion into the cell that occurs against a concentration gradient.
- The process by which ions cross the root from the epidermis to the xylem with the expenditure of metabolic energy against the gradient of their concentration.
- Unlike passive transport, this type of movement requires energy (the nutrient is moved into the root by a "carrier" molecule or ion).
- Thermodynamically absorption of ions against electro-chemical potential gradient.
- Thus, this process requires the presence of living aerobically respiring cells.
- The process is inhibited by metabolic inhibitors and there is some sort of selectivity ion is observed in the process.
- The various carrier like ribonucleo-proteins (nucleic acid bind cation and proteins bind anions), cell mitochondria etc. bind ions selectively and after formation of such carrier-ion complexes, they cross membranes and other barriers not permeable to free ions. After the transfer is accomplished, the ion-carrier complex is broken, the ion is released into the inner space of cell and the carrier become free.

Theories or pathways and mechanisms of ion uptake

There are different mechanisms by which the nutrients are taken in, they include;

1. Carbonic acid exchange theory
2. Bennet-Clark's protein lecithin theory

3. Contact exchange theory
4. Donnan's equilibrium theory
5. Ion pumps and ATPases
6. Carrier hypothesis
7. Lundegardh theory (Electro-chemical theory)

1. Carbonic acid exchange theory:

- 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 (H_2CO_3) 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.

2. Bennet-Clark's protein lecithin theory:

- In 1856, Bennet-Clark suggested that because the cell membranes 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 group of cations and anions.
- According to this theory;
  a) Phosphate group in the phosphatide is regarded as the active center binding the cations and the basic choline group as the anion binding centre.
  b) The ions are liberated on the inner surface of the membrane by decomposition of lecithin by the enzyme lecithinase.
  c) 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.

3. Contact exchange theory:

- According to this theory the ions adsorbed or 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 over by the oscillation volume of ions adsorbed on clay particles, and the ions adsorbed on clay particles may be exchanged with ions adsorbed on root surface directly without first being dissolved in soil solution.

4. Donnan's equilibrium theory:

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

5. Ion pumps and ATPases:

- ATP is the energy currency of plants.
- The ATPases are a group of enzymes located on the plant cell membrane.
- ATP splits into ADP and inorganic phosphate (Pi) with energy release as,

ATP ---------- ADP + Pi + energy

- The energy released is utilized for operation of H^+ pumps to transport ions to the plant cell.

6. Carrier hypothesis:

- **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 an activated carrier proteins present on the membrane which combined with the ion at the outer surface of the plasmalemma and form ion-carrier complex.
- This carrier-ion complex moves across the semipermeable membrane and reaches the inner space by the expenditure of energy.
- On the inner side of the membrane *i.e.*, within the cytoplasm, due to some chemical changes, the membrane-ion complex breaks to release the ions.
- The released ion can not leak because the membrane is impermeable to free ions.
- On releasing the ion, the carrier moves out of the cytoplasm or moves back to the outer surface of the membrane where it can again combine with an ion to form a complex.
- 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.

7. Lundegardh theory (Electro-chemical theory):

- Electro-chemical theory was proposed by **H.L. Lundegardh (1945).**
- Describes flow or passage of electrons cause movement of anions from outside to inside.
- Owing to the negative charge of the protoplasmic membrane, cations pass without difficulty into the protoplasm.
- Whereas, the uptake of anions requires energy supply.
- Oxidation processes seem to supply this energy.
- Thus anions (A^+) are actively absorbed via a cytochrome pump and cations (M^+) are passively absorbed.

Nutrient mobility within plant

- An important characteristic of some nutrients is the ability to move within the plant tissue.
- In general, when certain nutrients are deficient in the plant tissue, that nutrient is able translocate from older leaves to younger leaves where that nutrient is needed for growth.
- Nutrients with this ability are said to be mobile nutrients, and include **nitrogen, phosphorus, potassium, magnesium, and molybdenum**.
- In contrast, immobile nutrients do not have the ability to translocate from old to new growth.
- Immobile nutrients include **calcium, sulfur, boron, copper, iron, manganese, and zinc.**
- Nutrient mobility, or immobility, provides us with special clues when diagnosing deficiency symptoms.
- If the deficiency symptom appears **first in the old growth**, we know that the deficient nutrient is **mobile.**
- On the other hand, if the symptom appears in **new growth**, the deficient nutrient is **immobile.**

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