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Mechanisms of Nutrient Uptake and Assimilation Processes in Some Plants: A Review

Idris Z. Kiri

Department of Biological Sciences,
Sule Lamido University,
P.M.B. 048,
Kafin Hausa

Email: idriskiri@slu.edu.ng

Abstract

Nutrient demands of plants are fulfilled via nutrient uptake by the roots, even though minor quantities of certain nutrients might be assimilated via leaves. For the reason that the majority of nutrients are assimilated by roots, an understanding of root morphology and cell structure is crucial in knowing this basic plant process. Nutrient achievement by plants hinges on ion applications on superficial, root assimilation capacity, and plant requirement. Movement of ion in plant cells is classified into active and passive. Ion concentrations in the cytoplasm of plant cells are frequently and considerably observed to be greater than in soil solutions. Consequently, roots ought to be able to take up ions in contrast to broadly diverse concentration gradients. Currently, two major theories of ion transport across membranes are reported in literature: carrier theory where carrier agents accountable for transferring ions from one side of membrane to the other; encounter specific ions for which they have attraction, form carrier ion complexes; and move across membranes and connecting ATPase theory of ion transport; which is related with the plasmalemma and is activated by cations; the ion pump theory, which is a demanding proces, transporting via electrochemical gradient. Measurements of ion uptake could be achieved through tracer techniques. Long-distance transport of ions to shoots happens in the vascular system, with water being the transporting agent. New and stimulating developments in mineral uptake mechanism of plants have momentously added to our understanding of the function of nutrients uptake in plants. Most research comparative to physiology of nutrient uptake has been conducted under controlled environment by means of particular nutrient cultures in the growth medium.

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

Introduction

Nutrients are dimensionally and transitory varied in the soil and, hence, plants have advanced to have great and small attraction transporters for uptake athwart nutrient concentration gradients (Shin *et al.*, 2004; Griffiths *et al.*, 2021). Nutrient acquisition by plants is intricate and energetic because soil, climate and plant factors and interactions are concerned (Wilfahrt *et al.*, 2021). Most studies on physiology of mineral nutrient acquisition have been conducted under controlled environments using specific nutrient cultures in the growth medium. Such studies, as observed by Fageria *et al.* (2006) and Jayakumar *et al.* (2019), are crucial for knowing elementary values of nutrient uptake and assimilation; but could lack some vital characteristics once plants are cultivated in field environments for commercial commitment. Nutrient absorption via roots is the main machinery to fulfil

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**Author for Correspondence*

nutritive requisite of plants, even though little quantities of some nutrients may be absorbed through leaves if applied as foliar sprays or are pollutants in the atmosphere (Barber, 1995; Alaoui *et al.*, 2022). In unique conditions such as wherever deficiencies must be relieved instantly, these micro-nutrients are applied through the leaves (Rajasekar *et al.*, 2017). The fact that majority of nutrients are absorbed by roots, discussion of root morphology and cell structure is fundamental in understanding nutrient uptake processes in plants. Hence, the objective of this paper is to review root morphology, active and passive ion transport, ion uptake mechanisms, carrier ion transport theory, ATpase theory of ion transport, ion absorption measurement, and ion translocated from roots to shoots.

Root morphology

Plant roots accomplish significant roles as they not only serve the function of holding the plant in position, but also absorb water and nutrients from the soil, and are the location where useful and morbific organisms interact in the rhizosphere (Paez-Garcia *et al.*, 2015). Plant root system is in charge of acquiring soil resources (Louvieaux *et al.*, 2020). Significant characters of root morphology include root hairs (Marin *et al.*, 2021), epidermis (Takada and Iida, 2014; Nyainleta *et al.*, 2022), cortex (Kim *et al.*, 2022), and stele (Tomescu, 2021). In the process of their absorption, ions transfer via epidermis, cortex, endodermis, and stele and drain into the xylem after which the ions are carried from the xylem to shoots (Bao *et al.*, 2019). Photosynthetic assimilates are conveyed by phloem tissue from the leaves and shoots to roots in the course of plant development (De Schepper *et al.*, 2013; Liesche and Patrick, 2017; Babst *et al.*, 2022). There are two analogous routes for solute transportation, through cortex cells, before reaching stele and they are passageway through extracellular location or apoplast cell walls and intercellular locations, and; passage from cell to cell in the symplast via plasmodesmata to cellular particles and to vacuole sections inside cells (Marschner, 1995; Kim *et al.*, 2018; Aubry *et al.*, 2019).

Effective or active nutrient uptake takes place across cells bounded by membranes. Vacuoles, nuclei, chloroplasts, ribosomes, and mitochondria are implanted within cells (Mengel and Kirkby, 1978; Mathur, 2020). Plasma membranes attach to the cytoplasm and cell wall, whereas tonoplast membranes distinct the cytoplasm from the vacuole; plasmalemma membranes form borders between cells and the external medium, and it is these membranes (not cell walls) that make active barriers against uptake of ions and molecules suspended in aqueous outer media (Gronnier *et al.*, 2018; Ackermann and Stanislas, 2020).Plant cell organs that execute specific roles accelerating plant growth and development include vacuoles, which perform the function of water economy of cells as well as providing locations for separating of water end products of metabolism (Meyer *et al.*, 2010; Hedrich, 2012; Jiang *et al.*, 2021); chloroplast, which are places for light energy conversion and CO_2 assimilation (Bose *et al.*, 2017; Song *et al.*, 2021); mitochondria, which enclose enzymes monitoring numerous stages of metabolism such as the tricarboxylic acid (TCA) cycle, respiration, and fatty acid metabolism (Jacoby *et al.*, 2012; Taylor, 2018; Wang *et al.*, 2022); ribosomes, which are supermolecular assemblies comprised of ribosomal nucleic acids and proteins empowering production of polypeptides from free amino acids (Martinez-Seidel *et a*l., 2020); plasmodesmata (PD) are fenced plant cell wall networks that permit the transport of molecules between cells and perform significant functions throughout plant development and in the arrangement of cellular and systemic signaling responses throughout the period of communications of plants with the living and non-living environment (Huang and Heinlein, 2022).

Biological membranes are made up of protein and lipid molecules (Jacobson *et al.*, 2019)

In almost equivalent sizes and about 7 to 10mm thick. Biological membranes are not totally impervious and such may permit diffusion of hydrophilic ion and molecules but the degree of perviousness rest on constituents building up the membranes (Mengel and Kirkby, 1978; Watson, 2015; Kalkan and Eşrefoğlu, 2022). A unit membrane model was suggested by Danielli and Davson (1935), in which individual unit contains binary lipid molecules layers with their hydrophobic ends (fatty acids) slanted to innermost (Marschner, 1995; Watanabe *et al.*, 2019). Singer (1972) propositioned a membrane model comprising largely of liquid amphiphilic existing in the model. Lipids and proteins may be compelled by electrostatic, H, and aquaphobic link (Mengel and Kirkby, 1978; Pöyry and Vattulainen, 2016; Noack and Jaillais, 2020). Walker (1976) reported that certain proteins may even spread over membranes to form protein networks from one side of a membrane to another (Cournia *et al.*, 2015; Chatzigoulas and Cournia, 2022). These protein networks can be considered hydrophilic openings through which polar solutes such as ions can be translocated (Corradi *et al.*, 2019).

Active and passive ion transports

Ion transportation in plants is accomplished in two ways and they include active and passive ion transports, with each having its distinct characteristics. Active ion transport is characterized by ions moving against concentration gradients (Stillwell, 2013; Griffiths and York, 2020). Ion movement depends onelectrochemical potential gradients and the attractions of cations and anions to negative electropote-ntials and positive electropotentials, respectively (Alaoui *et al.*, 2022). Passive ion transport is categorized by movement of ions from higher to lower concentrations or down chemical gradients of potential energy (Tomkins *et al.*, 2021).

It should be observed that, electrochemical potentials are recognized through membranes due to uneven charge allocations (Kisnieriene *et al.*, 2019). Discrepancies between membrane potentials and actual potentials formed by non-equilibrium allocations is a degree of quality of energy needed (Fageria *et al.*, 2006; Baklouti *et al.*, 2023). Electrical charge , therefore could be computed by means of a revised Nernst equation explained by Ting (1982), as stated below:

$$\Psi = (-RT/ZF/In\ (ai/a_0)$$

Where Ψ = electrochemical potential between root cells and external solutions in mullivolts (MV); R = gas constant (8.3J/mol K); T = absolute temperature (K); Z = net charge on ion (dimension less); F = Faraday constant (96, 400 J/mol); a_i = activity of ion inside a tissue, and a_0 = activity of ion outside a tissue. For speedy computations, it is expedient to recall that RT/F = 26 mV (Fageria *et al.*, 2006; Farhangi-Abriz and Ghassemi-Golezani, 2023).

Measurement of electrochemical potential

Measurement of electrochemical potential in cells and external media is valuable because it helps in understanding ionic concentrations in cells and the external media. Secondly, it suggests whether ions are transported actively or passively (Fageria *et al.*, 2006; Farhangi-Abriz, and Ghassemi-Golezani, 2023). When Nernst equation is employed in computing electrical potentials, negative values designate passive uptake and positive values show passive uptake for anions (Mengel and Kirkby, 1978; Ciribelli *et al.*, 2020). Measurements are only effective when equilibrium state is sustained in the system, which according to Fageria *et al.* (2006), is difficult under practical situations. Hodges (1973) stated that electrical potential variances across tonoplasma membranes are in the range of -60 to -200 mV (cytoplasm negative), and electrical potential variances athwart tonoplasts are relatively low at 0 to -20mV, with cytoplasm values being negative compared to vacuole values (Vodeneev *et al.*, 2015; Lyu and Lazár, 2017; Kowacz and Pollack, 2020).

The mechanisms of ion uptake

The kinetic outline of ion uptake rates athwart roots, known as ion influx isotherms, were initially recognized in the 1960s by the pioneer study of Emanuel Epstein with 86Rb or 42K radioactive tracers for potassium uptake in barley (Le Deunff *et al.*, 2016).

Ion uptake mechanism is best understood when ions are more concentrated in the cytoplasm than in soil solutions, and extreme cases may be 10, 000 –fold higher (Alaoui *et al.*, 2022). In view of this, plant roots must be able to absorb ions against widely diverse concentration gradient; a particular ion involves metabolic energy for it to move ion against concentration gradients or against electrochemical gradient; and in such circumstance it is labeled as active uptake (Griffiths and York, 2020). There are two major theories of ion transport across membrane, now described in literature, and are the carrier theory and the ion pump theory (Mengel and Kirkby, 1978; Hedrich, 2012; Ragel *et al.*, 2019; Unsuree *et al.*, 2021).

Carrier ion transport theory

The carrier ion transport theory refers to agents in charge of transferring ions from one part of membranes to the another (Lombard, 2014; Stillwell, 2016; Wang *et al.*, 2018). Carrier proteins have properties comparable to that of enzymes, though, unlike enzymes, they have not been sequestered and categorized (Heinemann *et al.*, 2021). Currently, quantifying the actions of the carriers has not been realized (Eisenberg, 1990; Alberts *et al.*, 2002; Fageria *et al.*, 2006; Grabarczyka *et al.*, 2015; Gyimesi and Hediger, 2022). The carrier theory states that carriers encounter specific ions for which they have attraction, from carrier ion centres, and pass across membranes, then, the enzyme *phosphatase* situated at innermost membrane-bound increases, splits off phosphate from carrier complexes, and ions are discharged (Mengel and Kirkby, 1978; Alaoui *et al.*, 2022). Marschner (1995) and (Tyutereva *et al.*, 2022) observed that, in this transport process, energy is essential and participation of adenosine triphosphate (ATP) is usually recounted. Fageria *et al.* (2006) and Griffiths and York (2020) reported that high energy molecule ATP is produced from adenosine diphosphate (ADP) = inorganic P (Pi) from respiration (oxidative phosphorylation reactions).

The following equations describe the mechanism of the uptake (Mengel and Kirkby, 1978) as in Fageria *et al.* (2006):

$$\text{Carrier} + \xrightarrow{\text{Kinase}} \text{Carrier P} + \text{ADP} \qquad (1.2)$$

$$\text{Carrier P} + \text{Ion} \longrightarrow \text{Carrier P} - \text{Ion} \qquad (1.3)$$

$$\text{Carrier P} - \text{Ion} \xrightarrow[\text{Phosphatase}]{} \text{Carrier} + \text{Pi} + \text{Ion} \qquad (1.4)$$

$$\text{Net: Ion} + \text{ATP} \xrightarrow{\text{Transport}} \text{Ion} + \text{ADP} + \text{Pi} \qquad (1.5)$$

ATPase theory of ion transport

Prior to early 1970s, little or nothing was known about the ATPpase theory of ion transport in plants (Palmgren and Morsomme, 2019). Hodges (1973) proposed an ATpase theory of ion transport in plants. Later, the method was labeled by Mengel and Kirkby (1978) and Clarkson (1984). Fageria *et al.* (2006) and Kabała and Janicka (2023) reported that ATpase is a group of enzymes having the ability to break ATP into ADP and Pi, and energy released from these reactions can be used in ion transport across membrane- a process known as activation of ATP, and which is connected with the plasmalemma and triggered cations (Hodges *et al.*, 1972; Falhof *et al.*, 2016; Zharova *et al.*, 2023).

The kinetics of ion uptake

This is an enzyme kinetic hypothesis related to membrane transport. Various reviewers like Clarkson and Hanson (1980); Epstein (1973); Nissen (1974); Nissen *et al.* (1980); Fageria (1984), Griffiths and York (2020) have discussed widely on ion uptake kinetic, and designated it as transport of ions into plants cells; which may be comparable to association between attachment of substrates to enzymes and discharge of their products subsequent to catalysis (Epstein and Hagen, 1952). Segel (1968), Robinson (2015) and Mu *et al.*, 2020 posited that complete order of activities in enzyme catalyzed reaction is:

$$S \longleftrightarrow E$$

The above may be represented as

$$E + S \leftrightarrow E\,S \leftrightarrow EX \leftrightarrow EY \leftrightarrow EZ \leftrightarrow E - P \leftrightarrow P + E$$

The enzyme (E) first combines with substrate (S) to form an enzyme substrate complex (ES). On the surface of enzymes, substrates may go through one or more intermediate forms (X, Y, Z) and lastly transformed to an ultimate product (P) (Segel, 1968; Robinson, 2015; Udema, 2023). The final product separates permitting free enzymes (E) to activate again. The next step is wherein uptake by plants follows hyperbolic relationships with growing concentrations (Up to ~ 200 mmol/m^3) in the growth medium (Ingestad, 1982; Overman, 2012). Uptake rates at given concentrations can be projected as: $V = (V_{max}\,C_i) / (K_m + C_i)$ Where V_{max} = maximum velocity, C_i = concentration of ion in the growth medium, and K_m = Michalis constant equal to substrate ion concentration giving half maximal rates of uptake. Small values or K_m indicate high attraction between ion and carrier; straight lines are generally attained if uptake rates and concentrations are plotted as reciprocates (Clarkson, 1974; Khan, 2021); plotting rates of uptake (V) against V/C and V_{max} occur so that V_{max}/K_m can be extrapolation of experimental slopes to the ordinates and abscissas, and or extrapolation of these lines offer intercepts at $1/V_{max}$, the concentration at half maximal velocity equivalent to K_m.

Ion absorption in otherm has been defined to be comparative to 1_{max}, K_m, and E with the projected equation

$$1_{max} = (1_{max}\,C_i) / (K_m + C_i - C_{min}) \qquad (1.7)$$

Where 1_{max} =maximum net entry of ions into roots, nmol.m^{-2}, S^{-2}, C_{min} = value of C_{10} (C_{10} = ion concentration in solution at the root surface, mmol. L^{-1}) where = influx and h = O, mmol. L^{-1}) (Barber, 1995). At concentrations above zero, uptake rates were discovered to be zero and was consequently called efflux (E) from roots (Barber, 1995). It is important to note that ion uptake kinetic values differ with plant age, nutrient concentration, temperature, root morphology, plant demand for nutrients, and analytical technique used to make measurements (Fageria *et al.*, 2006; Meychik *et al.*, 2021). An uninterrupted flow method for measuring nutrient uptake kinetics, by Hai and Laudelout (1966), Fageria (1973, 1976), Fageria *et al.* (2006) and Baiyin *et al.* (2021) described, is established on the fact that rates of nutrient uptake (U) are equivalent to products of flow rate (F) and variances between concentrations of solutions entering systems (Co) and those of outgoing solutions (C_s).

The importance of solution flow rates in smooth culture trials and that of the definite flow rates essential for a specific experiment will rest on type and intensity of ion, plant stage of development, productivity of roots in absorbing verified ions, and circumstances of research (Edward and Asher, 1974; Baiyin *et al.*, 2021). According to Clarkson (1984) the reaction of 1_{max} and K_m in the transport method to physical and metabolic influences can offer certain perception into the overall nature of procedures stirring ions through membranes. Association between ion and concentration and consumption rate were reported to be more complex when concentrations differed over extensive scopes (Epstein *et al.*, 1963; Griffiths and York, 2020). Mechanisms were proposed to work in sequences, one at the plasmalemma and one at the vacuolar membrane or tonoplast (Laties, 1969; Alaoui *et al.*, 2022). Uptake mechanisms go on unaffected over varied concentration series, but their features adjust at definite distinct outside concentrations (Nissen, 1974; Le Deunff *et al.*, 2016; Saibi and Brini, 2021). Ion absorption data were revisited in many plant species and it was concluded that ion uptake in higher plants can be explained by multiphasic mechanisms which account for ostensible opposing evidence for analogous and sequence models (Nissen *et al.*, 1980; Wang *et al.*, 2023).

Methods for measuring ion uptake

The most popular methods of measuring ion uptake or absorption are by tracer techniques that use excised roots. The major limitation of these techniques is that they tend to overlook huge quantities of ion carried across roots into the xylem and lastly to shoots. This is to say that, in reality, only little percentage of nutrients absorbed are reserved in roots, and greater percentage are transferred to shoots (Asher and Ozanne, 1967; Loneragan and Snowball, 1969, Chalk and Smith, 2020). Consequently, determination of ions in both roots and shoots should be carried out in ion absorption experiments (Fageria *et al.*, 2006; Abdolzadeh *et al.*, 2008; Griffiths and York, 2020). Chemical evaluations are repeatedly in use to calculate amounts of nutrient absorption by roots, and this is attributed to approximating fluctuations in nutrient composition in both roots and shoots. The absorption method is attained by finding the average of the values over some days (Pitman, 1976; Lamshoeft *et al.*, 2018). The rate of monovalent cation uptake is usually greater than that of polyvalent cations in crop plants (Fageria, 1973; Belatus, 2018). Monovolent ions are absorbed more rapidly than divalent or polyvalent ions of analogous hydrated radii and ions of small radii are absorbed quicker than ions with great hydrated radii (Fageria *et al.*, 2006; Bhardwaj *et al.*, 2020).

Uptake rates from nutrient solution of 100-day old rice plants were examined to be much greater for K^+ compared to Mg^{2+}. These disparities in uptake rates prove that uptake mechanisms for K^+ are more applicable and discriminating than for Mg^{2+} (Zhang *et al.*, 2017). Also, efficient uptake mechanisms ought to occur for NO_3^- and HPO_4^-, and presumably for NH_4^+ and Cl^-. Plant cells demand these dynamic uptake machineries to propel appropriate inorganic ions in a short period; which are crucial for great plant growth rates. Although NO_3^-, NH_4^+, and HPO_4^- are required for production of many organic compounds, great amounts of K^+ are criterion for optimum stimulation of several enzymes and stability of cellular osmotic concentrations (Zhu *et al.*, 2021). Dry matter of undeveloped tissues was described as having greater concentrations of N, P and K than grown up tissue (Mengel, 1974b; Burns, 1992; Reddy *et al.*, 2000; Sitienei *et al.*, 2013; Souri *et al.*, 2019). Certain corporeal attributes of ions effect their rates of uptake. The most significant of these attributes are charge and hydrated radii (Hiatt and Leggett, 1974; Gransee and Führs, 2013; Griffiths and York, 2020).

How ions are transported from roots to shoots

The mechanism of ion transport from roots to shoots can be described through the following steps: the first step is that of absorption of ions by roots. Long-distance transport of ions to shoot transpires in the vascular system of the xylem and phloem, and principally in the xylem vessels with water being conveying agent (Fageria *et al.*, 2006; Alaoui *et al.*, 2022). Xylem transport is motivated by gradients in hydrostatic pressure in roots. Notwithstanding gradients in water potential and solute movement in the xylem from roots to shoots is one-way, long-distance transport of solutes in the phloem, which has living sieve tubes, is two-way; increase in transportation rates of plants improve both uptake and translocation of mineral nutrients in the xylem (Marschner, 1995; Schenk *et al.*, 2020). Tanner and Beevers

(1990) and Blevins (1994) reported that transpiration of water hastens movement of greatest elements in the xylem, but transpiration is not essential for movement of ions in the xylem. Concentrations of many elements (e.g., K and P) were higher in phloem sap than in xylem sap (Blevins, 1994; Killiny, 2019). Nitrate, Mn, and B are comparatively phloem steady (Fageria *et al*., 2006; Renseigné *et al*., 2007). According to Larcher (1995) the rate-limiting phases in the nutrient translocation chain are uptake, conduction, and liberations of ions by the symplast into roots, as the transpiration stream is usually capable of transporting high amounts of mineral nutrients. Larcher (1995) also reported that nutrients absorbed by roots can be moved adequately to the shoots, even if velocity of the transpiration stream in the xylem is low. The phloem plays a fundamental role in distribution of nutrients. Phloem and xylem tissues are connected at many locations onward the transport system, predominantly in roots and nodes of stem (Schuetz *et al*., 2013; Liesche and Patrick, 2017).

Conclusion

The uptake or acquirement of nutrients by plants is active and multifaceted. Absorption kinetics are generally more vital than thermodynamics in recounting uptake. It should be noted that rates of nutrient absorption by roots are determined by nutrient providers to root surfaces, active absorption by roots and plant request for nutrient from the xylem, ions are transported to growing organs in shoots for metabolic processing. Energy is mandatory for this process, which is provided through respiration. Kinetic evidence is providing acumens into nature of ion carriers. Most ion uptake studies have been of short duration in solution culture experiments using excised roots. An important constituent of ion uptake in higher plants is the existence of electrogenic proton pumps, which encompass plasmalemma. Movements of cations such as K+ possibly happen through membrane networks and down electrochemical gradients. Although not hitherto copiously categorized, carriers for anions such as nitrate occur. Nitrate uptake is inducible in roots of advanced plants.

New and exciting development in mineral nutrient research in the past few decades have greatly contributed to our understanding of the role of essential nutrients in improving yields of annual crops. However, research in mineral uptake of crops in not without obstacles. Most research relative to physiology of nutrient acquisition has been conducted under controlled environment using specific nutrient cultures in the growth medium. Such research may lack some important aspects when plants are growth under field conditions for economic purpose. Nutrient concentrations, temperature, pH, humidity, diseases, insects, and weeds can be controlled when plants are grown in controlled environments. Controlling these factors at an appropriate level is difficult in field conditions. In view of this, the following recommendations are proffered:

(i) The shortcomings attributed to research conducted in controlled experiments should be taken into consideration each time plants are grown under field conditions. This is because, controlled experiments, being so artificial compared to field experiments, should not serve as a basis for drawing general conclusion;

(ii) For proper or further understanding of nutrient uptake process in plants, relevant data, drawn from correlated fields of physiology, biochemistry, climatology, and evolution, should be collected and fully exploited.

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