16 Plant Nutrition
Rates of Transport and Metabolism

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CONTENTS

16.1 INTRODUCTION

Leonardo da Vinci stated that "*Nessuna certezza è dove non si pò applicare una delle scienzie matematiche, over che non sono unite con esse matematiche*," that is, "There is no certainty where one is not able to apply one of the mathematical sciences, or that they are not united with mathematics" (Da Vinci, 1952). The present chapter focuses on quantitative rates of various kinds to give the reader a clearer sense of some of the many processes that involve essential nutrients and some other elements absorbed by plants. Green plants obtain carbon from the air, whereas organisms such as fungi obtain carbon as saprophytes, breaking down organic materials of living or dead organisms. Some fungi, on the other hand, have evolved to form mycorrhizae with the roots of green, vascular plants. Unicellular and multicellular photosynthetic, nonvascular plants such as some algae obtain carbon and other essential elements with little transport from the environment to the site of photosynthesis. In algae, compared to vascular plants, the products of photosynthesis are transported relatively short distances to become new living tissue or to be expelled from the plant to the

environment. Vascular plants, on the other hand, have evolved to move essential plant nutrients within the xylem and the phloem over distances far greater than the dimensions of the uncharged atoms, molecules, or ions of the essential plant nutrients. The anatomy of vascular plants, as well as nonvascular plants, can be understood to include sources and sinks, out of, into, and among which essential nutrients move. Within the context of an ecosystem, a living plant can be viewed as a sink which, as a result of the organizing force of DNA, is the recipient of essential nutrients of the plant that originate from the environment, which can be considered a source. Within ecosystems, living plants also act as sources of elements that flow outside the plant by processes such as transpiration, root exudation, shedding of flowers, fruit and seeds, and consumption and transport of vegetative tissue, fruit, storage organs, and seeds by animals. When a plant dies, it becomes a source of essential nutrients that are released at various rates of decomposition to other organisms in the ecosystem. Dead plants can be considered sources of essential plant nutrients that can be released by decomposition to the environment, which, in this case, can be considered a sink.

Several means of measuring rates of transport of essential nutrients in plants, other than distance per unit time, or velocity, include volume transfer ($cm^3\ h^{-1}$), mass transfer ($g\ h^{-1}$), and specific mass transfer ($g\ cm^{-2}\ h^{-1}$) (Canny, 1960). Specific rates include velocity per unit area, volume, or weight of plant tissue. This chapter is divided into units to facilitate access to data and information. The subject matter of some of the references could be placed in more than one subchapter, but such subject matter has, for simplicity, generally been placed in only one subchapter.

16.2 RATES OF ABSORPTION OF ESSENTIAL NUTRIENTS BY PLANTS

16.2.1 Algae

Flynn et al. (2018) investigated the effects of growth rate, cell size, motion, and elemental stoichiometry on nutrient kinetics in three algal species, that is, the coccolithophorid *Emiliania huxleri*, the raphidophyte *Heterosigma carterae*, and the diatom *Thalassiosira weisflogii*. Using data from six sources, they compiled values of some nitrogen (N) rate transport variables for the three algal species, including (variable, verbose variable, units):

- NCT_{Gmax}, N transport rate expressed per cell-C required to support $G = G_{max}$, g N (g C) $^{-1}$ d^{-1}.
- NCT_{max}, Maximum possible N transport rate expressed per cell-C, g N $(g\ C)^{-1}\ d^{-1}$.
- $TNcell_{Gmax}$, N transport rate expressed per cell required to support $\mu = \mu_{max}$, pg N $cell^{-1}\ d^{-1}$.
- $TNcell_{max}$, maximum possible N transport rate expressed per cell, pg N $cell^{-1}\ d^{-1}$.

Many other variables and data useful for those interested in the kinetics of transport of nutrients across cellular membranes are included in the report by Flynn et al. (2018).

Two transport systems for nitrate (NO_3^-) in the acidophilic thermophilic alga *Cyanidium caldarium*, strain 0206, were studied by Fuggi et al. (1984). In an external basal medium adjusted to pH 3, within the range of external concentration of 0–2 mM NO_3^-, after pretreatment of NO_3^- limitation or of NO_3^- excess (30 mM), a low-affinity system and a high-affinity system of absorption were measured. At external concentrations of NO_3^- < 1 mM, the high-affinity system was saturated. The low-affinity system was saturated only at high NO_3^- concentrations (K_m = 0.45 ± 0.10 mM). Within the range of external concentration of 0–2 mM NO_3^-, the function estimating the rate of NO_3^- uptake (μmol min^{-1} mL^{-1} packed cells) was curvilinear for both treatments, but a constant rate of uptake occurred at about 1 mM NO_3^- with NO_3^- limitation, whereas the NO_3^- uptake continued to increase from 0 to about 1.5 mM NO_3^- with NO_3^- excess. Comparing uptake at pH 3 and pH 7, the high-affinity system was active only at acid pH and was inactive at neutral pH, whereas the low-affinity system was active both at acid and neutral pH.

C. caldarium is microscopic red alga that is found in acidic hot streams, bogs, and moist acidic soils. It contains the photosynthetic pigment, phycoerythrin, in addition to chlorophyll. Rigano et al. (1992) subjected the alga to conditions of nutrient sufficiency, or deficiency of N, P, or K and measured concentrations of amino acids produced by the alga in response to the nutritional environment. Glutamate was the dominant amino acid (AA) in nutrient-sufficient cells (11.2 μmol mL^{-1} packed cell volume (pcv)], in N-limited cells (7.71 μmol mL^{-1} pcv), and in P-limited cells (7.46 μmol mL^{-1} pcv); however, in K-limited cells, the dominant AA was alanine (8.83 μmol mL^{-1} pcv). The rate of ammonium (NH_4^+) uptake by nutrient-sufficient cells was 182 ± 6.08 μmol NH_4^+ h^{-1} mL^{-1} pcv, and values of the corresponding rates of uptake of NH_4^+ are 462 ± 13.2 for N-limited, 193 ± 11 for K-limited cells supplied with K^+, and 75 ± 2.25 for P-limited cells supplied with inorganic phosphorus (P_i). Detailed data and information regarding the amounts of specific AAs accumulated by the cells (μmol mL^{-1} pcv) in response to the four different nutritional environments are included by Rigano et al.

In the freshwater alga *Selenastrum minutum* (Naeg.) Collins (UTEX 2459), the rate of NH_4^+ assimilation was set as the independent variable, and the relationship between NH_4^+ assimilation rate and in vivo activity of phosphoenolpyruvate carboxylase (PEPC) was determined. A linear relationship of 0.3 mol C fixed via PEPC per mol N assimilated was observed, agreeing well with the PEPC requirement for the synthesis of the amino acids found in total cellular protein. As the activity of PEPC increased with increasing rates of N assimilation, there was a corresponding increase in the level of PEPC activators (glutamine, dihydroxyacetone phosphate), an increase in glutamine (GLN)/glutamic acid (GLU) ratio, and a decrease in the level of PEPC inhibitors (2-oxoglutarate, malate). The dark carbon fixation rate, described by a linear function (slope = 0.3 mole (mol) C·mol N, $r^2 = 0.991$), increased from 10 to 60 μmol mg^{-1} chlorophyll (Chl) h^{-1} when the NH_4^+ assimilation rate was increased from 0 to about 170 μmol mg^{-1} Chl h^{-1}. The GLN/GLU ratio increased from 0 to 0.7 as NH_4^+ assimilation rate was increased from 0 to about 170 μmol mg^{-1} Chl h^{-1} (Vanlerberghe et al., 1990).

Ammonium ion was shown to induce the suppression of photosynthetic carbon fixation from about 300 to 150 μmol dissolved inorganic carbon (DIC) mg^{-1} chlorophyll h^{-1} at a range of irradiance in the range of 100 to 1000 μE m^{-2} s^{-1} in an N-limited green alga, *S. minutum* (Naeg.) Collins. The culture cuvette was maintained at 21.5°C, DIC was 4.7 mM, and chlorophyll (Chl) was 1.5 μg^{-1} Chl mL^{-1} (Guy et al., 1989).

16.2.2 Vascular Plants

Vascular plants absorb essential nutrients as uncharged atoms or molecules, ions or nanoparticles through the roots, and stomates and cuticle of leaves or stems and can translocate these chemical species relatively large distances within the plant, compared to the dimensions of the chemical species absorbed.

16.2.2.1 Roots

Within a range of concentrations from 0.1 to 10,000 mmol m^{-3}, net rates of uptake of calcium (Ca^{2+}), potassium (K^+), N, P, sulfur (S), and zinc (Zn^{2+}) were found to range from less than 0.001 to greater than 1.0 μmol g fresh weight (FW) $root^{-1}$ h^{-1} (Pitman, 1975).

Radial transport of low concentrations of NH_4^+ through the apoplastic transport pathway (ATP) and symplastic transport pathway (STP) to the xylem in root tissue was mediated mainly by the epidermal NH_4^+ transporter 1;3 (AMT1;3) (Duan et al., 2018). However, apoplastic transport controlled by AMT1;2 at the endodermis prevailed at high external concentrations of NH_4^+. AMT1;2 favored N allocation to the shoot, and the investigators concluded that the ATP is of major importance in the partitioning of N absorbed as NH_4^+ to the shoot. They present numerous figures showing relationships between normalized shoot ^{15}N accumulation (μmol g^{-1} root DW h^{-1}), symplastic and apoplastic pathways, and AMT1;2 and AMT1;3 transporters.

Using a ^{15}N isotope tracer technique and the root systems of plants growing in a semi-arid steppe environment of the Tibetan Plateau, the objective of Hong et al. (2018) was to determine the root traits (root biomass, volume, surface area, average diameter, length, specific root length, and specific root area) that make the largest contribution to the total uptake of N (^{15}N-NO_3^-, ^{15}N-NH_4^+, and ^{15}N-glycine) of 10 alpine plant species. Two grasses, a sedge, four forbs, and three legumes were used, and N uptake rates were calculated per unit dry shoot mass (μmol ^{15}N g^{-1} dry shoot mass d^{-1}). Short-term ^{15}N isotope labeling experimental data indicated that different plant species had different preferences for forms of N. For the 10 plant species, the N source and range of values of N uptake rate (μmol ^{15}N g^{-1} dry shoot mass d^{-1}) measured are: ^{15}N-NH_4^+ (0.05–3.56), ^{15}N-NO_3^- (0.09–6.69), ^{15}N-glycine (0.11–2.66) and total N (0.25–12.92). The monocotyledons (grasses and sedges) had significantly greater ($P < 0.05$) N uptake rates of ^{15}N-NO_3^-, ^{15}N-NH_4^+, and ^{15}N-glycine and total N than did the dicotyledons (forbs and legumes).

To describe the localization of NO_3^- absorption and translocation within morphological regions of the corn root, Lazof et al. (1992) divided the corn root into six regions beginning at the root tip, that is, 0–5 mm, 5–15 mm, 15–35 mm, 35-lats (region of varying length, terminating basally at a point 20 mm below the first visible emerging lateral root), basal-primary (primary root above the same point with lateral roots removed), and lateral roots. They used $^{15}NO_3^-$ to measure rates of absorption and translocation of $^{15}NO_3^-$ when the roots were supplied 0.1 mM or 10 mM $^{15}NO_3^-$. The cumulative rate of ^{15}N accumulation in each of the six root regions over 15 min was in the range of 40–400 μmol (g DW_{tiss})$^{-1}$ h^{-1}, and the rates per gram of fresh weight of the tissue were lowest at the root tip and highest in the lateral roots. Tabular data are presented by Lazof et al. for each region, indicating distribution of the NO_3^- unidirectional flux density (pmol mm^{-2} h^{-1}) among the six morphological regions of the 7-day-old corn root.

16.2.2.2 Leaves

Organic liquids (Stålfelt, 1916), and particularly oils (Turrell, 1947) with low surface tension, undoubtedly

infiltrate stomata. Aqueous solutions with a surface tension near that of pure water (approximately 72 dyne cm^{-1}) do not penetrate (Greene and Bukovac, 1974). In contrast, stomatal penetration of aqueous solutions has been demonstrated in the laboratory when the surface tension is lowered sufficiently with surfactants (Dybing and Currier, 1961). Using fluorescent and radioactive tracers and a precipitation method to investigate foliar penetration of aqueous solutions, Dybing and Currier found that stomatal penetration by aqueous solutions occurred rapidly if an efficient surfactant was used at the proper concentration. Surfactants varied in their ability to promote stomatal entry, and the concentration of surfactant necessary for stomatal penetration varied with the species being tested. The leaves of *Zebrina pendula* Schnizl., *Pyrus communis* L., *Prunus armeniaca* L., and *Lactuca scariola* L. were readily penetrated via stomata. Leaves of *Phaseolus vulgaris* L., however, required a greater concentration of surfactant for stomatal entry, and cuticular penetration through areas over the veins took place quite rapidly. Rates of stomatal penetration of *Zebrina* leaves by ^{14}C-labeled urea during a 5-min period were 234 counts per minute (cpm) with 0.1% Vatsol surfactant and 6 cpm with no surfactant with open stomates. With closed stomates, corresponding rates of penetration were 2 cpm with 0.1% Vatsol surfactant and 4 cpm with no surfactant. Rates of penetration of *Zebrina* leaves by $H_3P^{32}O_4$ during a 5-min period were 787 cpm with 0.1% Vatsol surfactant and155 cpm with no surfactant with stomates open and 321 cpm with 0.1% Vatsol surfactant and 175 cpm with no surfactant with stomates closed (Dybing and Currier, 1961).

The rate of absorption of carbon from the air as CO_2, measured by net assimilation rate (NAR), was increased in *P. vulgaris* (bean) by application of gibberellic acid, urea, and sugar sprays (Alvim, P. de T., 1960). The application of all three substances resulted in NAR of 0.044 g dm^{-2} d^{-1}, compared to 0.035 g dm^{-2} d^{-1} of the control. The application of urea alone resulted in NAR of 0.029 g dm^{-2} d^{-1}. Analysis of variance indicated that NAR was significantly ($P < 0.01$) increased by gibberellic acid or by sugar treatment, but that effects of the following treatments were statistically insignificant regarding rate of carbon assimilation (measured by NAR): urea, and interactions of gibberellic acid × sugar, gibberellic acid × urea, sugar × urea, and gibberellic acid × sugar × urea.

Using an artificial system based upon the use of a polysulfone membrane and a potassium hydroxide (KOH) sink to mimic acquisition of CO_2 from the atmosphere that occurs through stomates, Nogalska et al. (2017) achieved efficiency of their CO_2 capture system similar to a range of rates of carbon CO_2 assimilation. The purpose of their artificial system is to capture CO_2 from the atmosphere through a porous membrane and then to pass the CO_2 to other compartments to be finally converted to methanol by electro-reduction or to hydrocarbons for use as fuel in fuel cells. The assimilation of CO_2 includes uptake through stomates by the process of diffusion and can reach between 15 and 40 μmol m^{-2} s^{-1}. In a range of 0–120 min, CO_2 flux across the artificial membrane began at 160 μmol CO_2 m^{-2} s^{-1}, rapidly declined to about 80 μmol CO_2 m^{-2} s^{-1} at 10 min, 40 μmol CO_2 m^{-2} s^{-1} at 20 min, 25 μmol CO_2 m^{-2} s^{-1} at 40 min, 20 μmol CO_2 m^{-2} s^{-1} at 60 min, and continuing to gradually approach an asymptote (constant rate) about of 20 μmol CO_2 m^{-2} s^{-1} at 120 min.

Foliar absorption of trivalent iron ($^{59}Fe^{3+}$, or iron (III)) was studied with tomato, sorghum, kidney bean, and small white bean. Total stomatal area per unit leaf area was found to be a major factor in determining the rate of foliar uptake of $^{59}Fe^{3+}$ per unit dry weight (DW) or per unit of leaf area. There were distinct differences in rates of uptake of $^{59}Fe^{3+}$ by the four different plant species. The use of a surfactant caused a large increase in $^{59}Fe^{3+}$ uptake in both the sorghum and the red kidney bean leaves during the day. An increase also occurred due to the surfactant for the sorghum during the night. The essentially linear rate of uptake for the first 30–40 min followed by a sharp decrease in rate is highly suggestive of a mass flow mechanism. The sharp decrease in uptake rate may occur due to the filling of the sub-stomatal chamber with treatment solution. The poorer agreement between species as submersion time increases can be explained as an expression of internal leaf characteristics, such as the size of the sub-stomatal chamber and the arrangement of the mesophyll cells surrounding the chamber (Eddings and Brown, 1967).

Studying cuticles of tomato fruit, with no stomatal pores, and onion leaves, with stomatal pores, Yamada et al. (1964) found that $^{45}Ca^{2+}$, rubidium ($^{86}Rb^{+}$, an analogue for K^{+}), chlorine ($^{36}Cl^{-}$), and sulfate ($^{35}SO_4^{2-}$) moved more rapidly from the outside of the cuticle to the inside of the cuticle, compared to movement of the ions from inside the cuticle to outside. Moreover, they found that during a 40-h period, the rate of movement of the four ions was initially rapid, declining with time. They concluded that the permeability of the cuticular membranes to these four ions was greater from outside to inside, compared to permeability of the cuticles from inside to outside. They observed that these differences were greater in the tomato fruit cuticle, which lacks stomata, than in the cuticle of the green onion leaf, which possesses stomata. Penetration of the monovalent cations was investigated using isolated leave cuticles of apricot (*P. armenaica* L). The penetration rates of the monovalent cations in group IA followed a normal lyotropic series, that is, cesium (Cs^{+}) > Rb^{+} > K^{+} > sodium (Na^{+}) > lithium (Li^{+}). Absorption of 1 mM

Rb^+ and phosphate by leaves of bean seedlings occurred during a 24-h period at constant rates. Rates were constant at 0.785 and 6.81 mμmol cm^{-2} leaf h^{-1} for phosphate and Rb^+, respectively (McFarlane and Berry, 1974). The absorption rates were obtained as the slopes of the linear regressions calculated by the least square method (Jyung and Wittwer, 1964).

Absorption, assimilation, translocation, and distribution of N from urea applied in the autumn to leaves of 1-year-old potted Fuji/M6 apple (*Malus domestica* Borkh) trees was investigated by painting the leaves with 3% urea solution (enriched to 10 atom% with ^{15}N) or water (control trees) (Dong et al., 2002). Most uptake of ^{15}N by the leaves occurred during the first two days, during which the mean rate of absorption of 0.29 g ^{15}N m^{-2} d^{-1}. From 2 to 4 d after application of urea, the absorption rate decreased to 0.03 g m^{-2} d^{-1}, and the absorption rate decreased to 0.002 g m^{-2} d^{-1} by 7 d, after which the rate was "negligible." During the first 4 d after application of urea, the mean rate of increase of amino acid concentration was about 275 mg kg^{-1} d^{-1} in the leaves, 112 kg^{-1} d^{-1} in the bark, and 25 kg^{-1} d^{-1} in the bark.

The foliar absorption of four chemical species containing N [NO_3^--^{15}N, NH_4^+-^{15}N, urea ($CO(NH_2)_2$)- ^{15}N or ^{13}C and ^{15}N dual-labeled glycine (NH_2CH_2COOH)] and translocation from leaves to roots were investigated using two Mediterranean forest tree species, that is, *Quercus ilex* and *Pinus halepensis*. Seedlings were grown 14 months after germination in 305-ml pots filled with fertilized peat, N/P/K 14/16/18 + micronutrients. Nitrate and $CO(NH_2)_2$ were supplied as free forms, NO_3^- was supplied as KNO_3, and NH_4^+ was supplied as ammonium sulfate [$(NH_4)_2SO_4$]. All N was supplied at a concentration of 40 mM N. The foliar absorption rate of N (mg m^{-2} d^{-1}) for each tree species was calculated on a whole-plant basis and plotted as a linear function of cuticular conductance (g_c, mmol m^{-2} s^{-1}) for each N treatment. The *y*-intercept and slope for *Q. ilex* were greater than for *P. halepensis* for each N treatment, indicating that for any value of cuticular conductance, N was absorbed more rapidly by *Q. ilex* than by *P. halepensis*. The rate of N absorption from urea was about three times higher than from the other N forms. No statistical differences among N absorption rates were found for the other three N forms, but N absorption rate tended to decrease in the following order: $NH_4^+ \geq NH_2CH_2COOH \geq NO_3^-$ (Uscola et al., 2014).

In another study using *Q. ilex* and *P. halepensis*, uptake of N by the roots was measured using 1mM N solutions containing labeled N as NH_4^+, NO_3^-, or NH_2CH_2COOH, that is, $(^{15}NH_4)_2SO_4$, $K^{15}NO_3$, or $^{15}NH_2{}^{13}CH_2{}^{13}COOH$ (Uscola et al., 2017). Ammonium and NH_2CH_2COOH were absorbed by the roots at a similar rate, but faster than NO_3^- in both species, and intact, dual-labeled glycine was found in both species, proving that both species can absorb at least one compound containing intact organic N.

A study was conducted to determine responses of poikilochlorophyllous *Stipa tenacissima* (esparto grass) and photoprotective *Rosmarinus officinalis* (rosemary) to foliar fertilization with P, Fe, Mn, or Zn before a rainfall event (Ruiz-Navarro et al., 2019). P and Zn fertilizer treatments in *R. officinalis* led to increases in the rate of photosynthesis (A, μmol m^{-2} s^{-1}). P fertilization resulted in lower stomatal conductance (g_s, mmol m^{-2} s^{-1}), suggesting to Ruiz-Navarro et al. that foliar fertilization with P resulted in more fine-tuned control of transpiration. Fe and Mn foliar fertilization improved poikilochlorophylly in *S. tenacissima*, and P and Zn fertilization improved photoprotection in *R. officinalis*, in both cases enabling more efficient use of the water pulse, compared to nonfertilized plants.

16.3 FACTORS AFFECTING RATES OF MOVEMENT OF ESSENTIAL NUTRIENTS WITHIN PLANTS

Two categories of movement of essential elements in vascular plants are (1) short-distance transport or movement across membranes of cells and organelles such as the plasmalemma, mitochondrion and vacuoles and (2) longer-distance transport through the vascular system composed of xylem and phloem. White (2012a) reviews environmental, physiological, and developmental factors in the entry of nutrients to the extracellular space (apoplast) of roots, transport of nutrients across the plasma membrane and tonoplast of root cells, and the pathways of movement into the xylem. He describes with text, tables, and figures the structure and composition of cellular membranes, energetics of the solute transport across the membranes, kinetics, and mechanisms of transport across the membranes, and genetic identity of proteins that facilitate transport of the nutrients across both the plasma membrane and tonoplast.

16.3.1 Saturation Kinetics

Rates and patterns of ion absorption by plant roots from the soil solution are partially influenced by the concentration of the elements outside the plant roots or, in the case of nonvascular plants, outside the cell membranes that are in contact with the environment. The concept of saturation kinetics was first observed in 1937 by Dutch plant physiologist T. H. Van den Honert (1937) who studied phosphate uptake by sugar cane (*Saccharum officinarum* L.) and found that as the concentration of phosphate outside the plant increased, it finally reached a maximum

rate of absorption. Subsequently, Emanuel Epstein and C. E. Hagen (1952) described the transport of ions across cellular membranes in terms used in enzymology. They observed that as with enzyme systems, saturation kinetics occurred as the concentration of a nutrient ion was increased outside a cell membrane. The rate of absorption in one direction across a plant cell membrane, v, if there is no counter-flow in the opposite direction can be expressed as the product of capacity and intensity factors: $v = (V_{max} \cdot [S])/(K_m + [S])$ This Michaelis–Menten equation relating the rate of enzymatic catalysis to the concentration of substrate was found by Epstein and Hagen (1952) to be equally valid to describe the rate of movement of an ion across a cell membrane as a function of the concentration of the ion outside the membrane, $[S]$. In the case when the rate of absorption of the ion is one-half the maximal rate, $v = ½\ V_{max}$. So, $V_{max}/2) = (V_{max} \cdot [S])/(K_m + [S])$, $(K_m + [S]) = 2[S]$, and $K_m = [S]$. Thus, K_m, the "Michaelis constant" equals the concentration of the substrate ion resulting in one-half the maximal rate of absorption. The lower the value of K_m for an ion, the higher is the affinity of the carrier sites for the ion (Epstein, 1972).

In subsequent work, Epstein et al. (1963) demonstrated that during the absorption of K^+ by barley roots, when increasing the concentration of K^+ in the substrate from 0 to 50 mM, the rate of absorption of K^+ increased, plateaued, then increased, plateaued at a higher rate, and so on until the maximal rate was reached at a concentration of 50 mM. This research pointed to more than one mechanism controlling the absorption of potassium across barley root cell membranes. Such experimental results were explained by Epstein et al. (1963) as being the result of one uptake mechanism ("Mechanism 1") prominent at the plasmalemma, or cell membrane, when substrate concentrations were on the order of 2×10^{-6} M, whereas a second mechanism or additional mechanisms were operative when absorption of K was from substrates with K^+ concentrations between 0.50 and 50 mM. Mechanism 1 obeys simple Michaelis–Menten kinetics, whereas absorption by Mechanism 2 at higher concentrations is a result of a more complex set of mechanisms. The rate, v, of uptake of K^+ corresponding to the range of substrate concentrations from 0 to 50 mM is approximately 0 to 40 μmol g^{-1} h^{-1}. Welch and Epstein (1968, 1969) concluded that both Mechanisms 1 and 2 exist in parallel across the plasmalemma. A thorough review of mechanisms of potassium uptake in plants (Cuin et al., 2008) indicates that there is a functional overlap between the high- and low-affinity mechanisms of K^+ uptake in plants and that K^+ can be absorbed via different kinds of channels in cell membranes. Following the pioneering work of Epstein et al. (1963), subsequent research has linked such factors as root:shoot ratio and relative growth rate (RGR) to nutrient uptake rate (v), maximum uptake rate (v_{max}), and uptake rate of the whole plant (v_{plant}) (Gutshick and Pushnik, 2005). For Zn^{2+}, a table summarizing values of Michaelis–Menten kinetics variables through membranes shows V_{max} in a range from 2.3 to 18,300 nmol [DW] g^{-1} h^{-1} (Broadley et al., 2007). This broad range of maximum rate of movement of Zn^{2+} across membranes is collected from many investigators using various crop species under various conditions to measure Zn^{2+} flux.

Regulation of K^+ absorption in barley (*Hordeum vulgare* L.) roots was studied by Glass (1976) who measured plasmalemma influx isotherms for K^+ in the system I concentration range (0.01–0.32 mM). The influx of K^+ was shown to be sigmoidally related to internal K^+ concentration. Data of Glass indicate that influx rate declined in a curvilinear manner from about 5 μmol g^{-1} h^{-1} to about 1 μmol g^{-1} h^{-1} for a solution containing 0.16 mM potassium chloride (KCl) within a range of K^+ concentration in the roots increasing from about 40 to 110 μmol g^{-1}. Glass concludes that his experiments support an allosteric model for the regulation of K^+ influx in which the "carrier," or transporter is conceived as possessing a single external binding site for K^+ as well as four sites for allosteric control of influx.

Kinetic influx parameters were measured for NH_4^+, K^+, and dihydrogen phosphate ($H_2PO_4^-$) provided in nutrient solutions to roses (Mattson, 2007). Within a range of NH_4^+ concentration from 0 to 10,000 μM N, the maximum influx rate (I_{max}) was 11.5 pmol N cm^{-2} s^{-1}, and K_m was 1193 μM. Within a range of K^+ concentration from 0 to 4000 μM K, I_{max} was 4.47 K cm^{-2} s^{-1}, and K_m was 222 μM. Within a range of P concentration from 0 to 400 μM P, I_{max} was 0.07 pmol P cm^{-2} s^{-1}, and K_m was 64 μM. Mattson also presents figures with three-dimensional surfaces showing the relationship between concentration of the nutrient in solution (C_s, μM), and plant nutrient concentration (C_p, g 100 g^{-1} DW) on net influx (I_n, μmol g^{-1} h^{-1}) fit the equation, $I_{max} = MaxI_{max} \cdot e^{aCp}$, using nonlinear regression program, SAS Proc NLIN (SAS Institute, 2004).

16.3.2 External or Internal Concentration of the Nutrient Itself

Effects of the external concentration of nutrient ions upon the rates of uptake by plants have been demonstrated using the enzyme-kinetic hypothesis of ion absorption (Epstein, 1976). When "low-salt" roots grown in a nutrient-deficient medium are transferred to a solution containing the deficient ion, a transient high rate of absorption will be achieved. As the concentration of the ion inside the compartment (e.g., cell, organelle) increases, if the concentration of the ion in the compartment is maintained at an adequate level, the uptake rate can decline to a steady rate.

Other changes in uptake rates of nutrient ions are diurnal, such as the case of net NO_3^- uptake in perennial ryegrass following the peak of diurnal CO_2 fixation after a lag of 5–6 h (Clement et al., 1978) or circadian patterns of K^+ uptake in *Lemna gibba* (Kondo, 1982).

Uptake of inorganic phosphate, P_i, is affected by external P_i concentration. *Spirodela* aquatic plants of a control treatment that included phosphorus were exposed to 1000 μM P_i and absorbed phosphorus at a rate of 500 nmol g^{-1} fresh wt. h^{-1}, whereas when the same species of the control treatment were exposed to 1 μM P_i absorbed phosphorus at a rate of 20 nmol g^{-1} fresh wt. h^{-1}. *Spirodela* plants that had been deprived of phosphorus for 4 days and had a 30% reduced growth rate, but no marked symptoms of P deficiency, were exposed to 1000 μM P_i and absorbed P_i at a rate of 1200 nmol g^{-1} fresh wt. h^{-1}. At a lower concentration of 1 μM P_i, *Spirodela* plants that had been deprived of phosphorus for 4 days and had a 30% reduced growth rate, but no marked symptoms of P deficiency, absorbed P_i at a rate of 40 nmol g^{-1} fresh wt. h^{-1} (McPharlin, 1981).

The research reported more than 100 years ago by Brezeale (1906) indicated that when an inorganic nutrient was withheld from the roots of hydroponically grown wheat plants for a period of hours, the absorptive capacity of the element was increased several-fold. Brezeale showed that after 18 h without each of the following nutrients, uptake rates of four essential nutrients increased significantly: 3.3-fold for NO_3^-, 2.2-fold for Ca^{2+}, 4-fold for K^+, and 2.5-fold for P_i. According to Glass (2005), following resupply of a withheld nutrient, rapid reduction of the increased capacity to absorb the nutrient at a high rate occurs, and he surmises that if plants are able to rapidly "up-regulate" and "down-regulate" uptake rates of essential nutrients, plants may be able to minimize fluctuations of availability of essential nutrients within the plant. Since concentrations of the essential nutrients in soils may vary across orders of magnitude (Reisenauer, 1966), this flexibility on the part of plants may have contributed to their survival and evolution.

In a study of NO_3^- translocation by detopped corn (*Zea mays* L.) seedlings, Ezeta and Jackson (1975) used KNO_3 and KCl in nutrient solution to measure the effects of various factors on uptake and translocation of NO_3^- and Cl^-. Exposing detopped plants to concentrations of 0.5, 2.5, or 15 mM KNO_3 during 5 h, NO_3^- translocation rates increased to maxima of approximately 2.2, 4.0, and 4.5 μmol NO_3^- g^{-1} h^{-1}. For the subsequent 5 h, the seedlings were all exposed to 0.5 mM KCl, and the translocation rates decreased to less than 1 μmol NO_3^- g^{-1} h^{-1}.

Potassium previously absorbed in intact barley (*H. vulgare* L. cv Beecher) reduced in the short-term influx of ^{86}Rb-labeled K^+ into roots of barley seedlings (Johansen et al., 1970). Because the influx values were similar to those of net absorption rates into intact plants, Johansen et al. concluded that K efflux was negligible, compared to the influx. In a figure showing influx or net absorption into intact or excised barley roots over a 72-h treatment period, rates varied little around 11.5 μg atoms K g^{-1} fresh roots h^{-1} when roots were transferred to a solution containing no K, but rates initially decreased from 9 μg atoms K g^{-1} fresh roots h^{-1} when first immersed in a solution with 2000 μM KCl to a minimum of about 2 μg atoms K g^{-1} fresh roots h^{-1} at 24 h, then increased to about 5 μg atoms K g^{-1} fresh roots h^{-1} at 72 h.

Feedback regulation of NO_3^- influx through the inducible high-affinity transport system (IHATS) in excised roots of barley (*H. vulgare* L. cv Steoptoe) by NO_3^-, NO_2^- and NH_4^+ was demonstrated by using a wild-type and a mutant line Az12:Az70 (genotype nar1a;nar7w) (King et al., 1993). Changes in NO_3^- influx (μmol g^{-1} FW h^{-1}) via IHATS for NO_3^- (in the wild type and mutant) and NO_2^- (in the wild type) induced for influx from 0 to 7 days, in increments of 1 day, follow the pattern of increase in NO_3^- influx that increases from 0 d to 2 d, then decreases through 7 d. In addition to NO_3^-, NO_2^- and NH_4^+ were also able to exert feedback inhibition upon NO_3^- influx.

Transpiration, N uptake, and flows in the vascular system of maize (*Z. mays* L.) were found to be influenced both by the genotype of two inbred lines (N-efficient Zi330 and N-inefficient Chem94-11)—and by the concentration of N in the nutrient solution used to irrigate quartz sand in which the plants were grown (Niu et al., 2007). From the transfer of the plants to quartz sand at the two-leaf stage until the day of the first harvest, the plants were irrigated with a complete nutrient solution of which 4 mM N was supplied as 2 mM $Ca(NO_3)_2$-N. The high-N (HN, 4 mM $Ca(NO_3)_2$-N) and low-N (LN, 0.08 mM $Ca(NO_3)_2$-N) levels were applied to plants of the two genotypes on the day of the first harvest. From day 1 to day 10 after the first harvest, the transpiration rate (g water $plant^{-1}$ d^{-1}) of the N-inefficient genotype was lower with the LN treatment, compared to both genotypes with the HN treatment and the N-inefficient genotype at the HN treatment. N-efficient Zi330 had higher N uptake and N cycling within the plant when grown under N-limited conditions and had higher water use efficiency at both N levels. Under N-limited conditions, NO_3^- reduction was shifted from shoot to roots in both lines.

In a study on the sites, pathways, and mechanism of absorption of Cu–EDDS complex ([s,S′]-ethylene diamine disuccinic acid) in primary roots of maize (*Z. mays* L.), Niu et al. (2011) found that the absorption rate (μg cm^{-2} h^{-1}) of Cu–EDDS complex was greatest in the lateral root zone, less in the apical root zone and least in the maturation zone when Cu–EDDS was supplied to the roots at

either 200 μmol L^{-1} or 3000 μmol L^{-1}. They concluded that Cu–EDDS complex enters the root xylem passively, mainly through apoplastic spaces in lateral roots that serve as the main site of absorption. At low concentrations (<200 μmol L^{-1}), the Cu–EDDS complex diffuses across root apoplastic spaces into the root xylem, and sites where lateral roots penetrate the endodermis and cortex are the main paths of entry. Casparian strips form the main physical barrier. At high concentrations (<3000 μmol L^{-1}), passage cells – the physiological barriers that control ion absorption – are injured or killed and, with adjacent early metaxylem vessels, provide channels of entry for the Cu–EDDS complex into the root xylem.

In a study to evaluate the physiological effects of intracellular NO_3^- and prior NO_3^- nutrition on NO_3^- fluxes and the coordination of nitrate reductase activity (NRA) with NO_3^- influx activities, Zhang and MacKown (1993) eliminated the interaction of these processes with NO_3^- translocation by using cell-suspension cultures of *Nicotiana tabacum* L., cv KY14 (tobacco) instead of an intact plant system. Tobacco cells grown with complete Murashige and Skoog medium for 7 d were subcultured for 3 d with NH_4^+-free media containing 0, 5, 10, 20, 30, or 40 mM NO_3^-, and then cell NO_3^-, in vitro NRA, NO_3^- influx, and efflux of cell NO_3^- were determined. ^{14}N-NO_3^- efflux rate increased from 0 to about 2.5 μmol g fresh weight $(FW)^{-1}$ 10 min^{-1} as a linear function of cell NO_3^- concentration within the range of 0–60 μmol g NO_3^- g_{FW}^{-1}. Cells subcultured for 3 d with media initially containing 0, 5, and 20 NO_3^- had equivalent cell densities (about 156 mg FW mL^{-1}), but the corresponding NO_3^- concentrations in the cell were 0.06, 1.68, and 12.20 μmol g^{-1} FW, respectively, and the corresponding values of NRA were 8.8, 12.5, and 18.4 nmol g^{-1} FW min^{-1}.

16.3.3 Competing or Noncompeting Ions, Including H^+ (pH)

The absorption of the transition metal cations from concentrations approximately 1 μM is strongly inhibited by alkali and alkaline earth cations and by other transition metal cations (Robson and Pitman, 1983). The rate of zinc absorption by wheat roots was shown to have been decreased from about 300 ng atoms/g FW roots/day with no K^+ present to about 100 ng atoms/g FW roots/day 750 μM K^+ was present with the concentration of Ca^{2+} less than 1000 μM. The rate of K^+ absorption was approximately the same, about 30 ng atoms/g FW roots/day when Ca^{2+} was present, regardless of whether K^+ was present or not in the solution from which the zinc was absorbed. The assimilation of NO_3^- by barley seedlings was affected in several ways by the salinity of sodium chloride (NaCl) and sodium sulfate (Na_2SO_4) (Aslam et al., 1984). Both Cl^- and SO_4^{2-} salts severely inhibited uptake by the roots, as measured by μmol NO_3^- g^{-1} fresh wt h^{-1}, however reduction of NO_3^- and NO_2^- were much less affected by salinity in short-term studies of 12 h.

Aluminum (Al), a major stressor of plants in acidic soils, was found to decrease Fe in xylem sap in *Cucumber sativus* L. (cucumber) plants of two cultivars supplied with chelated Fe^{3+} in nutrient solution of pH 4.0, whereas Al increased ferric chelate reductase (FC-R) activity in plants that were not supplied Fe^{3+} (Bityutskii et al., 2017). In contrast, Fe^{3+} supplied in the nutrient solution mitigated the Al-induced increase in xylem sap Al. Of the two cultivars compared in this study, the cultivar Phoenix was deemed to be more Fe-efficient than the cultivar Solovei. In the +Fe, +Fe + Al, and –Fe treatments, 2 d after transfer from a nutritionally sufficient solution to the treatments, there were no significant differences of root FC-R activity (μmol Fe^{2+} g^{-1} DW h^{-1}). However, a significant (p <0.05, n = 4) difference in root FC-R activity between the two cultivars was measured for the -Fe + Al treatment: about 16.5 μmol Fe^{2+} g^{-1} DW h^{-1} for Solovei, compared to 5 μmol Fe^{2+} g^{-1} DW h^{-1} for Phoenix. At 7 d after transfer to treatment solutions, the cultivar Solovei demonstrated higher root FC-R activity for the -Fe and -Fe + Al treatments, compared to the cultivar Phoenix, and there were no significant differences in root FC-R activity among the two cultivars at 7 d after transfer to treatment solutions.

Calcium supplied as calcium sulfate or as calcium chloride was found to inhibit energy-dependent K^+ transport in excised roots of corn (*Z. mays* L.) (Elzam and Hodges, 1967). The rate of K^+ absorption increased, in typical hyperbolic isotherm that can be analyzed by Michaelis–Menten kinetics, from 0 to a maximum of about 1.2 μmol g^{-1} FW h^{-1} as a function of a range of K^+ concentration, 0 to 20 mM. When 0.05 mM Ca^{2+} was added to a solution from which the roots were absorbing K^+, the rate of K^+ absorption decreased to a maximum of about 0.10 μmol g^{-1} FW 10 min^{-1} at the high end of the range of 0–0.20 mM K^+, compared to a maximum rate of about 0.22 μmol g^{-1} FW 10 min^{-1} at 0.20 mM K^+ concentration without Ca^{2+}. Elzam and Hodges, citing other reports, note that Ca^{2+} inhibition of K^+ absorption in corn roots is similar in some respects to the inhibitory effect of Ca^{2+} on Na^+ and Li^+ absorption in several plant species.

Tungstate (WO_4^{2-}) is a toxic ion that has been shown to prevent the formation of NO_3^- reductase, thereby depriving the plant of NO_3^--N (Heimer et al., 1969). Heimer et al. were able to reverse tungstate inhibition of the formation of nitrate reductase by molybdate (MoO_4^{2-}) in tobacco XD cells. They demonstrated the inhibitory effect of WO_4^{2-} on development of NRA and uptake of NO_3^- in barley shoots by treating the barley seedlings for 5 d with

a Hoagland's solution containing either no WO_4^{2-}, 0.1 mM $NaWO_4$, or 0.5 mM $NaWO_4$ and then adding 3 mM NO_3^- at 0 h. During 24 h, shoots were harvested and assayed for NRA and NO_3^-. Higher levels of WO_4^{2-} inhibited root and shoot development as well as NO_3^- uptake. In another experiment, Heimer et al. reversed WO_4^{2-} inhibition of NRA by MoO_4^{2-} in tobacco XDR^{thr} cells that had been subcultured into M-1D medium containing 0.1 mM WO_4^{2-}, increasing NRA from 0 to about 450 mμmol NO_3^- reduced h^{-1} g^{-1} tissue after 9 h.

Effects of P deficiency on assimilation and transport of NO_3^- and $H_2PO_4^-$ in intact plants of castor bean (*Ricinus communis* L.) occurred both in xylem and phloem in a study by Jeschke et al. (1997). They used a multicompartment model as a context to show relationships between concentrations and fluxes of NO_3^-, reduced N, $H_2PO_4^-$ and organic P in various plant parts during a 9-d study. In control plants, 58% of total NO_3^- reduction occurred in leaf laminae, 40% in the root and 2% in stem and apical tissues. Assimilation of $H_2PO_4^-$ occurred in leaf laminae (54%), apical bud (6%), stem tissues (19%), and root (20%). Remobilization of P from older leaves, equal to 50% of xylem transport, occurred via shoot-to-root translocation in the phloem. Major sites of assimilation of $H_2PO_4^-$ include leaf laminae (50%), roots (26%), and apical bud (10%).

Excised roots of *Oryza sativa* L. cv. I.R.8 (rice) absorbed molybdate (MoO_4^{2-}) at diminished rates (μmol MoO_4^{2-} g^{-1} $(4\ h)^{-1}$) in the presence of 0.01 or 0.1 mM manganese (II) sulfate ($MnSO_4$), copper (II) sulfate ($CuSO_4$), zinc sulfate ($ZnSO_4$), ammonium chloride (NH_4Cl), or $(NH_4)_2SO_4$ (Kannan and Ramani, 1978). The rate of uptake of molybdenum (Mo) by excised roots of *O. sativa* in the presence of 0.01 or 0.1 mM iron (II) sulfate ($FeSO_4$) was greatly enhanced.

In a study with seedlings of sunflower (*Helianthus annuus* L. cv Frankasol), Nikolic and Römheld (2003) determined that NO_3^--induced Fe deficiency chlorosis was exclusively caused by inhibited uptake and translocation of Fe from roots to shoots due to high pH at the root surface. They found that the uptake rate of ^{59}Fe by the symplast of the sunflower leaf via the petiole for 2 h was identical, regardless of whether there was no NO_3^- or 6 mM NO_3^- in the apoplast supplying ^{59}Fe to plants that had been grown in NO_3^--free nutrient solution or in nutrient solution with 4mM NO_3^-, resulting in 5mM NO_3^- in the leaf apoplastic fluid.

Sodium was found to stimulate the growth of *Amaranthus tricolor* L. plants through enhanced NO_3^- assimilation (Ohta et al., 1989). Na-deficient plants of *A. tricolor* received either 0.5 mM NaCl or KCl, and within 24 h, nitrate reductase activity (NRA, μmol NO_2^- g^{-1} FW h^{-1}) doubled in the plants treated with NaCl, and the enhanced level was maintained thereafter. When the plants were exposed to 2 mM $^{15}NO_3^-$, total ^{15}N absorbed by the plants was greater in Na-treated plants than in K-treated plants. Within 24 h of N treatment. Ohta et al. concluded that application of sodium (Na) to Na-deficient *A. tricolor* plants promoted NO_3^- reduction and subsequent assimilation of NO_3^--N into protein, resulting in enhancement of growth.

Effects of K^+ deficiency on photosynthesis, chloroplast ultrastructure, reactive oxygen species (ROS), and antioxidant activities in maize (*Z. mays* L.) were studied by Qi et al. (2019). Using two inbred K-deficiency-tolerant ("K-tolerant") maize genotypes 90-21-3 and 099 and two K-deficiency-sensitive ("K-sensitive") genotypes, D937 and 835, four parameters were measured: transpiration rate (Tr, mmol m^{-2} s^{-1}), photosynthetic rate (P_n, μmol m^{-2} s^{-1}, stomatal conductance (G_s, mmol m^{-2} s^{-1}), and intercellular CO_2 concentration (C_i, μmol mol^{-1}). In addition, the authors present seven parameters associated with chlorophyll fluorescence for the four genotypes. The results of the experimentation of Qi et al. (2019) indicate that K-tolerant maize promoted antioxidant enzyme activities to maintain ROS homeostasis and suffered less oxidative damage on photosynthetic metabolism, maintaining regular photosynthesis under K-deficiency stress.

Respiration of roots of 8-day-old seedlings of cowpea [*Vigna unguiculata* (L.) Walp] was stimulated by NO_3^- provided as 10 mM sodium nitrate ($NaNO_3$) (Sasakawa and LaRue, 1986). The roots respired 0.6–0.8 mg CO_2 $plant^{-1}$ h^{-1} for growth and maintenance, but the addition of 10 mM NO_3^- to the root medium increased respiration by 20–30% during the following 6 h when the roots were in light but not when they were in the dark. Removal of NO_3^- from the root medium slowed the increase of root respiration. During 8 h after addition of 10 mM $NaNO_3$ to the root medium, nitrate reductase activity (NRA, nmol NO_2^- gfw^{-1} h^{-1}) increased in root, stem and leaf tissue, and the NRA rates in the range of 0 to 100 nmol NO_2^- gfw^{-1} h^{-1} were greatest in the leaves, less in the stem, and least in the roots during the 8-h period in which NRA rates were measured at 0, 2, 4, and 8 h.

Zinc deficiency is common in pistachio (*Pistacia vera*) trees grown on calcareous, saline, and sodic soils. A greenhouse study was conducted with pistachio seedlings (cv. "Badmi") by Tavallali (2016) to evaluate beneficial effects of Zn (0, 5, 10, and 20 mg Zn kg^{-1} soil) under non-saline (S0) or saline (800 (S1), 1600 (S2), 2400 (S3) and 3200 (S4) mg NaCl kg^{-1} soil) conditions. The following variables were measured: Mineral elements [K, Ca, Na, Mg, Zn, and Cl], hormones [abscisic acid (ABA), 3-indoleacetic acid (IAA), cytokinin], and osmoregulators [proline, glycine betaine (trimethylglycine), and choline]. Specific absorption rates (mg g^{-1} d^{-1}) (e.g. K, Ca,

and Zn) were greater when Zn was applied, compared to the control, Zn-deficient soil, at various levels of salinity. Application of Zn decreased the absorption rates of Na and Cl. Application of 10 mg Zn kg soil^{-1} significantly increased the specific utilization rate (g g^{-1} d^{-1}) of K, Na, Ca, Mg, Cl, and Zn, compared to the other rates of Zn application to Zn-deficient soil for all salinity treatments (S0, S1, S2, S3, and S4).

Vapor fluxes of CO_2, O_2, and water vapor from shoots of wild-type *H. vulgare* L. cv Steptoe (barley) were unequal, as affected by NO_3^- assimilation when wild-type plants were exposed to NO_3^-; O_2 evolution at high light exceeded CO_2 consumption by 26% and CO_2 evolution in the dark exceeded O_2 consumption by 25% (Bloom et al., 1989). In contrast, when NH_4^+ was provided as the sole source of N to the roots of the wild-type *H. vulgare* L. cv Steptoe or a mutant barley (*nar*1a;*nar*7w) deficient in both NADH and NAD(P)H nitrate reductases, photosynthetic and respiratory fluxes of O_2 were equal to those of CO_2. The authors present graphs of data showing net CO_2 influx and net O_2 efflux, with a range of –5 to 15 μmol m^{-2} s^{-1}, for NH_4^+ and NO_3^- treatments as functions of a range of 0–800 μL L^{-1} intercellular CO_2 concentration (C_i) or as a function of a range of 0–1600 μmol m^{-2} s^{-1} photosynthetic flux density (PFD).

Toxic concentrations of Na^+, Ca^{2+}, and Mg^{2+} in the solution around the roots of *Capsicum annuum* L. (pepper) during a 96-h experimental period decreased root hydraulic conductance to values below 1000 mg g^{-1} h^{-1} MPa^{-1} (Cabañero and Carvajal, 2007). Stomatal conductance (g_s, mmol m^{-2} s^{-1}) a measure of the rate of absorption of CO_2 and rate of efflux of O_2 by the leaves of *C. annuum* L. was found to decrease in the presence of excessive concentrations of K^+, Mg^{2+}, Ca^{2+}, or Na^+ in nutrient solution, compared to a nutritionally sufficient nutrient solution as the control. The absence of K^+ in the nutrient solution was associated with stomatal conductance (g_s flux) values greater than the control.

Because drip-irrigated rice (*O. sativa* L.) in calcareous soil exhibits signs of iron (Fe) deficiency, Zhang et al. (2019) investigated whether NH_4^+ would alleviate Fe deficiency in rice seedlings under calcareous conditions. Fe-deficiency-tolerant variety cv. "T43" and Fe-deficiency-sensitive variety cv. "T04" were used to conduct two independent experiments with exposure to NO_3^- or NH_4^+ under calcareous conditions. Compared to plants exposed to NH_4^+, leaves of plants exposed to NO_3^- displayed severe chlorosis and significantly lower chlorophyll content during Fe starvation. Root hydraulic conductance was greater when both genotypes were exposed to NH_4^+ (about 6 ×10^{-9} kg s^{-1}cm^{-1} mPa^{-1}), compared to when exposed to NO_3^- (about 3 ×10^{-9} kg s^{-1}cm^{-1} mPa^{-1}), and root water uptake rate during daytime was greater for NH_4^+-treated seedlings (about 3.75 g plant^{-1} h^{-1}) of both genotypes, compared to about 2.75 g plant^{-1} h^{-1} for T43 treated with NO_3^- and about 2.00 g plant^{-1} h^{-1} for T04 treated with NO_3^-. Zhang et al. concluded that NH_4^+-N alleviated Fe deficiency in rice seedlings under calcareous conditions by promoting Fe re-allocation in rice tissues and Fe transportation from roots to shoots.

The pH of the soil solution has been shown to affect the rate of absorption of potassium. In studying the effect of pH on absorption of K^+, Jefferies et al. (1969) found that maximal rates of absorption of K^+ by two species of liverworts occurred in the laboratory at pH values close to the pH of the natural environments from which the samples were collected. K^+ influx into *Cephalozia connivens* was maximal, approximately 0.5 pmol cm^{-2} s^{-1} at pH 5, but when the pH of the solution with which the liverworts were in contact was higher or lower than the pH of the environments in which the liverwort samples had been collected, the rate of K^+ uptake was less than the maximum. This research points to the evolution of the ability of plants to maximize the rate of acquisition of essential nutrients from the environments influenced by key factors such as pH of the solution in contact with the organs of the plant which absorb the nutrients directly from the environment.

16.3.4 Salinity, NaCl

In experimentation with NaCl concentration in the nutrient solution being increased from 1 mM NaCl (control) to 75 mM NaCl by 25 mM NaCl increments every two days for three days, *P. vulgaris* L cv. "Contender" (bean) plants were sampled on the fourth day after the final salt concentration was reached, that is, 8 d after the salt treatment began (Cabot et al., 2005). In the summer, the high-salinity treatment resulted in growth rates 31% less than those of the controls, and CO_2 assimilation rate (μmol m^{-2} s^{-1}), stomatal conductance (mol m^{-2} s^{-1}), and transpiration rates (mmol m^{-2} s^{-1}) reported by Cabot et al. for the bean plants treated with 75 mM NaCl were less than those of the control.

Investigating effects of moderate NaCl stress on rates of photorespiration in spinach (*Spinacia oleracea* L. cv. Matador) leaves, Di Martino et al. (1999) grew two groups of spinach plants in 3000 cm^{-3} pots containing a mixture of soil, peat, and sand (1:1:1) in a greenhouse under temperatures that varied between 20/30 °C (night/day) and irradiance that did not exceed 1000 μmol (quantum) m^{-2} s^{-1}. When five to six leaves were fully expanded, control plants received optimal watering conditions by restoring daily water losses by transpiration, and NaCl-stressed plants were irrigated with water containing 1% (m/v) NaCl. From day 12 to day 40 of treatment, Na^+

accumulated in the leaves of the NaCl-treated plants from about 4 g Na^+ kg^{-1} dry matter (d.m.) to about 45 g Na^+ kg^{-1} d.m. at day 40, while the net photosynthetic rate decreased from about 25 μmol m^{-2} s^{-1} on day 12 to about 5 μmol m^{-2} s^{-1} on day 40. Na^+ content of leaves of the plants receiving the control treatment remained constant at about 4 g Na^+ kg^{-1} d.m. from day 12 through day 40 while the net photosynthetic rate slightly increased from about 25 μmol m^{-2} s^{-1} on day 12 to about 26 μmol m^{-2} s^{-1} on day 20 and then decreased to about 19 μmol m^{-2} s^{-1} on day 40. Proline was accumulated in NaCl-stressed plants, its concentration being 7-fold and 11-fold higher than in controls, respectively, after 20 and 30 d of stress. Based on their measurements of electron transport rate (J_f, μmol m^{-2} s^{-1}) measured by fluorescence in the leaves of plants receiving the two treatments, when supplies of CO_2 (μmol mol^{-1}) and O_2 (μmol mol^{-1}) were eliminated (CO_2) or decreased (O_2), Di Martino et al. observed that deprivation of CO_2 resulted in decreased J_f with both treatments, but more in the control than in the NaCl treatment.

Investigating effects of NaCl on flows of N, mineral ions and on N reduction rate of whole plants of salt-sensitive bean (*P. vulgaris* L. cv Gabriella) and salt-tolerant cotton (*Gossypium hirsutum* L. cv Alala), Gouia et al. (1994) measured decreasing rates of NRA (μmol NO_2^- h^{-1} g^{-1} fresh weight) corresponding to increasing concentrations of 50 mM and 100 mM NaCl in standard culture solutions for both salt-sensitive bean plants and salt-tolerant cotton plants. Comparing NRA in vitro, treating extracts of the third leaf and root of bean and of cotton with mannitol or NaCl, NRA with the mannitol treatment changed little between 0 and 300 mosmol l^{-1} for both bean and cotton. However, for the third leaf extract of bean, as osmotic concentration increased from 0 to 600 mosmol L^{-1}, in vitro NRA decreased from about 4 to 1 μmol NO_2^- h^{-1} g^{-1} fresh weight and for the root extract of bean in vitro NRA decreased from about 1.5 to 0 μmol NO_2^- h^{-1} g^{-1} fresh weight. For the third leaf extract of salt-tolerant cotton, as osmotic concentration increased from 0 to 600 mosmol L^{-1}, in vitro NRA of the third leaf extract decreased from about 12.5 to 3 μmol NO_2^- h^{-1} g^{-1} fresh weight and for the root extract of cotton, in vitro NRA decreased from about 4.0 to 0 μmol NO_2^- h^{-1} g^{-1} fresh weight.

Studying solute balance of a maize (*Z. mays* L.) source leaf as affected by salt treatment, Lohaus et al. (2000) treated intact maize plants with a high concentration of NaCl (100 mol m^{-3}), compared to a control with no NaCl and analyzed phloem sap, apoplastic fluid, xylem sap, solutes from leaf and root tissues and the leachate for carbohydrates, amino acids, malate, and inorganic ions. The concentrations of Na^+ and Cl^- in the leaf apoplast remained low (about 4–5 mol m^{-3}) in the salt-treated plants, and concentrations of Na^+ and Cl^- in the phloem sap of salt-treated plants did not exceed 12 and 32 mol m^{-3}, respectively. About 13–36% of the Na^+ and Cl^- imported into the leaves through the xylem was exported by the phloem, indicating an important role of the phloem in controlling concentrations of Na+ and Cl^- in maize leaves. The xylem and phloem transportation rates (μmol g^{-1} FW of leaf h^{-1}) of Na, K, Cl, and N presented by the authors indicate that translocation rates of each element in the phloem were always less than the corresponding rate in the xylem.

Effects of salinity on NO_3^- influx, efflux, NO_3^- net uptake rate (NUR) and net N translocation to the shoot were assessed in a ^{15}N steady-state labeling experiment in the halophyte *Plantago maritima* L. grown for 14 d using solution supplied with 50, 100, or 200 mol m^{-3} NaCl or without NaCl (Rubinigg et al., 2003). Labeling periods of 5 min and 2 h were used to determine $^{15}NO_3^-$ influx and $^{15}NO_3^-$ NUR, and efflux was calculated from the difference between mean influx and NUR in each experiment giving three replicates. Rates of NO_3^- NUR and NO_3^- influx were within the ranges of about 7–9 and 11–14 μmol NO_3^- g^{-1} FW_{root} h^{-1}, respectively, over a period of 2.0–6.5 h and 0.5–8 h for NO_3^- NUR and NO_3^- influx, respectively. Mean influx:efflux ratio was unaffected at 50 and 100 mol m^{-3} NaCl but increased more than twofold at 200 mol m^{-3} NaCl.

Sodium fluxes, xylem transport of Na^+, and K^+/Na^+ selectivity in roots of intact seedlings of *H. vulgare*, cv. California Mariout (very salt tolerant) and *H. distichon*, cv. Villa (less salt-tolerant) were studied by Wolf and Jeschke (1986). Except for xylem transport, all Na^+ fluxes and the cytoplasmic and vacuolar contents of Na^+ were higher in Villa than in the very salt-tolerant Mariout. At high external concentrations, xylem transport of Na^+ was substantially greater in Mariout than in Villa, and for both species, root-to-shoot Na^+ transport was almost independent of external concentration between 10 and 50 mol m^{-3} NaCl. For both genotypes at external Na^+ concentrations of 0.3, 1, 10, 20, and 50 mol m^{-3}, unidirectional Na^+ fluxes (μmol h^{-1} g^{-1} fresh weight (fr. wt.)) are presented for influx and efflux at the plasmalemma of cortical root cells, influx and efflux at the tonoplast, and transport to the shoot, along with corresponding values of cytoplasmic or vacuolar Na content in the roots (μmol g^{-1} fr. wt.). Wolf and Jeschke also present numerous figures related to their discussion of the kinetics of influx and efflux of Na^+.

Salt tolerance of Line 149 of durum wheat (*Triticum turgidum* L. subsp. *durum* Desf.) is explained by the presence of two genes for Na^+ exclusion, *Nax1* and *Nax2* (James et al., 2006). Using lines with or without the two genes, it was demonstrated that lines containing either *Nax1* or *Nax2* had lower rates of transport of Na^+ from roots to shoots than their near-isogenic pairs due to

lower rates of net loading the xylem, not to lower rates of net uptake from the soil or higher rates or translocation in the phloem. Moreover, lines with *Nax1* and *Nax2* also had greater rates of K^+ transport from roots to shoots, compared to rates of Na^+ transport from roots to shoots. Values of the transport rate (μmol g_{root} fresh weight^{-1} d^{-1}) of Na^+ from root to shoot were 6.5 for the *+Nax1* line and 22.5 for the *–Nax1* line. Evidence of the effect of the Nax2 gene in reducing transport of Na^+ from roots to shoots is similarly clear. The values of the transport rate (μmol g_{root} fresh weight^{-1} d^{-1}) of Na^+ from root to shoot were 9.7 for the *+Nax2* line and 17.9 for the *–Nax2* line.

16.3.5 Moisture Stress or Drought

Effects of abiotic stresses, that is, drought, heat, low CO_2 and high O_2, on the photosynthetic electron transport rate associated with the assimilation of the essential plant nutrient carbon as CO_2, photorespiration, and volatile isoprenoid emission were examined by Dani et al. (2014). Comparing drought-tolerant *Eucalyptus occidentalis* and drought-sensitive *Eucalyptus camaldulensis*, rates of stomatal conductance (mol m^{-1} s^{-1}), transpiration (mmol m^{-1} s^{-1}), net assimilation (μmol m^{-1} s^{-1}), isoprene emission (nmol m^{-2} s^{-1}) and monoterpene emission (pmol m^{-2} s^{-1}) are presented in graphs for a range of drought stress from 100% to 20% field capacity at two different O_2 concentrations, 2% and 20%. Rates of stomatal conductance, transpiration, and net assimilation were greater for drought-tolerant *E. occidentalis* than for *E. camaldulensis* throughout the range of drought stress at both O_2 levels. At 2% O_2, the rates of isoprene and monoterpene emission were generally less for *E. occidentalis* than for *E. camaldulensis* throughout the range of drought stress to which the two *Eucalyptus* species were exposed.

In a study of the effects of moisture stress and N fertilization on plant water use efficiency (WUE, g L^{-1}) in tomato (*Lycopersicon esculentum* L., var. Qianxi), Wang et al. (2018) applied soil treatments to vary moisture stress (90%, 70%, and 50% soil water-holding capacity) and low (NL, 1.0 g N pot^{-1}), medium (NM, 2.0 g N pot^{-1}) or high (NH, 3.0 g N pot^{-1}) N level, with 20% of N being applied to the soil and the remaining 80% being split in 10 foliar applications, one every 5 d. Carbon assimilation by photosynthesis (A_n, μmol m^{-2} s^{-1}) was affected very little by the water treatments, however A_n was highest in the NH treatment, intermediate in the NM, and lowest in the NL treatment after 28 d after transplanting, although differences due to N treatment were not statistically different during most of the treatment period. Stomatal conductance (g_s, mol m^{-2} s^{-1}) was significantly decreased by the severely water-stressed treatment, compared with the two other soil water treatments during most of the treatment period, and as a consequence, WUE was greatest in the severely water-stressed treatment, intermediate in the moderately stressed treatment, and least in the high soil water treatment. Wang et al. also found that reduced soil water regimes caused partial closure of stomata and intensified root-to-shoot ABA signaling, resulting in improved intrinsic water use efficiency (WUE_i, A_n/g_s). Based upon data from their experiment with tomato, they concluded that g_s, rather than N nutrition, was the primary determinant of WUE_p with fertigation.

White (2017) provides data and information regarding mechanisms of ion transport, proposed functions of the mechanisms, and corresponding gene symbol and gene number. A list of physical constants and definitions is included to facilitate understanding of his presentation of basic principles of the movement of ions, biochemical mechanisms for ion transport across membranes, and ion transport in the xylem and phloem.

16.3.6 Temperature and Radiant Energy

The rate of uptake of essential nutrients by a cell or whole plant is affected by temperature, and the temperature effects can be related to temperature coefficient (Q_{10}) values. The Q_{10} value represents the factor by which the rate of a reaction increases for every 10°C rise in the temperature. Absorption of the essential nutrients across cell membranes, as affected by temperature, can be categorized by absorptive processes with a Q_{10} of about 1–2, and another group of absorptive processes with a Q_{10} of 2 or greater. At a temperature of 1–2°C most absorption across cell membranes is thought to occur mainly by physical processes such as diffusion, mass flow, exchange, and adsorption. This physical absorption at low temperatures occurs rapidly, whereas metabolic absorption with a higher Q_{10} is prolonged. The amount of uptake of K^+ by washed carrot tissue slices increased from 0 μequiv/g fresh wt. to 4 μequiv/g fresh wt. from 2 to 6 h later at 2°C, the rate of uptake having gone to essentially zero at 2 h. On the other hand, the amount of K^+ absorbed continually increased from 0 μequiv/g fresh wt. to 16 μequiv/g fresh wt. at 20°C during the same 6-h period. As a function of temperature, from 2°C to 50°C, the amount of K^+ absorbed by washed carrot tissue slices increased during a 30-min period from about 4 μequiv/g fresh wt. to a maximum of about 7 μequiv/g fresh wt. at 40°C, but was about 5 μequiv/ g fresh wt. at 50°C. In contrast, when the temperature was raised more gradually during a 2-h period from 2°C to 50°C, the amount of K^+ absorbed by washed carrot tissue slices was only about 5 μequiv/g fresh wt. at 2°C and increased to about 12 μequiv/g fresh wt. at 40°C, but the amount of K^+ absorbed was only about 3 μequiv/g fresh wt. at 50°C (Sutcliffe

et al., 1962). These data showing the influence of temperature on the absorption of a monovalent ion, K^+, are indicative of the paramount importance of temperature in regulating rates of absorption of essential nutrients across cell membranes.

Because absorption of ions by the roots is an energy-consuming process, it is crucial that supplies of sugars from the leaves be available to provide energy for uptake of ions by the roots. The rate of absorption of K^+ by the roots of sunflower, *H. annuus*, was reduced from 0.140 mequiv h^{-1} to approximately 0.030 mequiv h^{-1} by cooling the stem of the plant from 25°C to 0°C to reduce downward translocation of sugars. The rate of uptake of K^+ returned to greater than 0.140 mequiv h^{-1} once the temperature of the phloem was returned to its original temperature (Weatherley, 1969). Weatherley interpreted the decrease in the rate of absorption of K^+ when the temperature of the phloem was lowered as a result of less sugar reaching the roots.

Temperature has also been shown to affect the uptake of P_i by *Spirodela*. When the aquatic plant species was exposed to 1000 μM P_i, the uptake rate decreased from 460 nmol g^{-1} fresh wt. h^{-1} at 25°C to 80 nmol g^{-1} fresh wt. h^{-1} at 5°C (McPharlin, 1981). Within the range of air temperature from 10°C to 35ºC, canopy CO_2 (mmol g DW^{-1} d^{-1}) assimilation of *Lactuca sativa* L. cv. "Black Seeded Simpson" (lettuce) increased in a linear manner at two different light levels, that is, 600 μmol m^{-2} s^{-1} and 1200 μmol m^{-2} s^{-1}, taking into account the fact that rates of photosynthesis at 10°C were about 40% less than at 35°C (Albornoz Gutierrez, 2013).

Investigating freezing tolerance of the basal nodes and roots of *Festuca pratensis* Huds, Darginavičienė et al. (2008) found that the rate of K^+Mg^{2+}-ATPase activity, as measured by accumulation of inorganic P (P_i, μmol/mg protein h^{-1}) was greater in the basal node plasmalemma than in the root cell plasmalemma on sampling dates of October 1, 2003, March 31, 2004, May 14, 2004, April 7, 2005, and May 26, 2005. In both nodes and roots, the highest K^+Mg^{2+}-ATPase activity was recorded early in the spring before the renewal of plant growth in late March. Other temporal aspects of K^+Mg^{2+}-ATPase activity in the plasmalemma of nodes and roots related to temperature are presented by the authors.

In a study of NO_3^- translocation by detopped corn (*Z. mays* L.) seedlings, Ezeta and Jackson (1975) exposed detopped plants to concentrations of 0.5 mM KNO_3 at 20, 30 or 40°C during the course of 6 h, NO_3^-, and translocation rates increased, approximately, from 2 to μmol NO_3^- g^{-1} h^{-1} at 20°C, from 4 to 12 μmol NO_3^- g^{-1} h^{-1} at 30°C, and from 3 to 9 μmol NO_3^- g^{-1} h^{-1} at 40°C. Other data are presented for the effect of the three temperatures on K^+ uptake rates and translocation rates of organic N.

Leffler et al. (2013) examined several root and shoot morphological characteristics and N absorption of several perennial and invasive annual grasses of the Great Basin of North America under various temperature conditions in growth chambers. They subjected their data to path analysis, which allows independent assessment of the importance of variables that are correlated with one another. One path model utilized links N uptake to root length and root mass, and the other path model links N uptake to leaf and root traits. Three rates of N absorption analyzed are mass-specific absorption rate (SAR_M, μg N g^{-1} root h^{-1}), area-specific absorption rate (SAR_A, μg N cm^{-2} root h^{-1}), and length-specific absorption rate (SAR_L, μg N m^{-1} root h^{-1}). At lower temperatures, N absorption by annuals and perennials was correlated with leaf N and mass, whereas at higher temperatures, uptake of N by annuals was correlated only with leaf traits, but uptake by perennials was correlated with leaf traits and root N and mass.

The effect of high temperatures on the assimilation of CO_2, metabolite content, and capacity for reducing power production in non-photorespiratory conditions was assessed by Pastenes and Horton (1996), using two bean (*P. vulgaris* L.) varieties, differing in their resistance to extremely high temperatures. Barbucho, a noncommercially bred Chilean variety, maintained photosynthetic functions for a longer period than did Blue Lake, a variety commercially available in the United Kingdom. Within the range of 20°C to 35°C, values of the rate of CO_2 assimilation increased in curvilinear functions from about 14 to 25 μmol CO_2 m^{-1} s^{-1} and transpiration rates increased from about 2 to 8 mmol H_2O m^{-2} s^{-1}. Based upon analysis of their experimental data, Pastenes and Horton suggest that limitations of the CO_2 assimilation rate are caused by metabolic restrictions that can be differentiated between those occurring in the range of 20°C to 30°C and 30°C to 35°C.

Absorption of Na^+ and K^+ ions by bean (*P. vulgaris* L.) stem tissue was studied by Rains (1969). Bean stem tissue was aged for at least 20 h by immersion in 0.5 mM $CaSO_4$ at 4°C, and when the stem tissue was subsequently exposed to a solution of 0.1 mM NaCl; 0.5 mM $CaSO_4$; pH 5.8 ±0.2; at 30°C. Subsequently, during 1 h, the absorption rate of Na^+ was 1.0 μmol g^{-1} h^{-1} regardless of the length of time of pretreatment from 0 to 24 h. When the pretreatment was done at 30°C, the Na^+ absorption rate dropped rapidly from 1.0 to about 0.1 μmol g^{-1} h^{-1}, corresponding to the range of 0–4 h of pretreatment and then continued at about 0.1 μmol g^{-1} h^{-1} from 4 to 20 h of absorption. In marked contrast, after 20 h of pretreatment with $CaSO_4$ at 4°C, when the absorption solution was 0.1 mM KCl; 0.5 mM $CaSO_4$; pH 5.8; at 30°C for 1 h, K^+ absorption was nil from 0 to 24 h for the 4°C pretreatment, but increased from 0 to a maximum of about 1.8

μmol g^{-1} h^{-1} at 20 h, then decreased to about 1.5 μmol g^{-1} h^{-1} at 24 h as a result of the 30°C pretreatment. Rains also experimented with effects of antimetabolites on Na^+ and K^+ absorption by bean stems and determined that the absorption of Na^+ by fresh tissue and K^+ by aged tissue was sensitive to antimetabolites, with K^+ uptake the more sensitive.

Diurnal rhythms of light and dark strongly influence the rate of absorption of ionic nutrients across cell membranes. Alberda (1948) showed that when the rate of absorption of phosphorus by maize plants was 0.20 mg P_2O_5 h^{-1} in the daylight, it decreased during a 4-h period to almost 0 mg P_2O_5 h^{-1} in darkness. When light was again supplied to the maize plants, the rate of uptake of phosphorus increased relatively rapidly during a 2-h period from about 0 mg P_2O_5 h^{-1} to 0.20 mg P_2O_5 h^{-1}, compared to the slower rate of decline. This experiment shows the importance of light as regards to uptake of the essential nutrients by photosynthetic plants and illustrates the diurnal fluctuation of the rate of uptake of phosphorus, as it is affected by diurnal changes in the presence and absence of light. In experiments with pea, Nobel (1969) showed that absorption of K^+ could be almost completely stopped by depriving pea plant leaf fragments of light. This finding indicates the importance of light for maximal absorption of fertilizer nutrients applied directly to leaves of crops.

Photosynthetic photon flux (PPF) was varied by Albornoz Gutierrez (2013) who found that in lettuce (*L. sativa* L), efficiency of CO_2 assimilation decreased with increasing PPF values from 0 to 2000 μmol m^{-2} s^{-1}, but he found that stomatal conductance (mol H_2O m^{-2} s^{-1}), net CO_2 assimilation (μmol CO_2 m^{-2} s^{-1}), and leaf transpiration (mmol H_2O m^{-2} s^{-1}) increased with increasing PPF values.

Irradiance response curves were developed by Fredeen et al. (1989) for the photosynthesis of fully expanded leaves of soybeans at ambient levels of CO_2 grown in growth chambers with high-P or low-P culture solutions. Data for 18 to 20 d after transplant show that both irradiance within the range of 0–2000 μmol quanta m^{-2} s^{-1} and availability of P in the culture solution affected the net photosynthetic rate (net PSR, the rate of assimilation of C) within a range of –2 to 15 μmol CO_2 m^{-2} s^{-1}. Increasing from 0 to about 250 μmol quanta m^{-2} s^{-1}, the increase in net PSR was rapid and approximately equal for both the high-P and low-P treatments. At values of irradiance above about 250 μmol quanta m^{-2} s^{-1}, net PSR was static at about 6 μmol CO_2 m^{-2} s^{-1}, whereas with the high-P treatment, at irradiance greater than 250 μmol quanta m^{-2} s^{-1}, net PSR increased to about 14 μmol CO_2 m^{-2} s^{-1} at 1000 μmol quanta m^{-2} s^{-1} and remained at that net PSR from 1000 to 2000 μmol quanta m^{-2} s^{-1}.

In a study of kiwifruit, Morandi et al. (2012) measured changes in xylem and phloem flows and transpiration rate as affected by short-period changes in weather conditions. They measured air temperature, relative humidity, solar radiation, and rainfall; they also calculated vapor pressure deficit (VPD). At 5 and 9 weeks after full bloom (WAFB), daily and hourly rates of xylem and transpiration flows were greatly reduced by low VPD (LVPD) conditions, while phloem flow was not affected by such changes during the entire season. LVPD conditions reduced morning shrinkage and slowed down afternoon growth rates of the fruit. In the early stages of kiwifruit berry growth, weather worsening (low irradiance, rainfall, and LVPD) reduced the (1) berry water exchanges by xylem and (2) transpiration but did not affect phloem imports to the fruit in the short term. Morandi et al. estimated a potential loss of about 0.8–1.0 mg Ca mg $fruit^{-1}$ d^{-1} due to low VPD conditions, since Ca is translocated only by the xylem to the fruit mainly occurring early in the season. They surmise that cloudy and/or rainy conditions during the early stages of kiwifruit development could result in diminished accumulation of Ca in the fruit and potential storage problems in the post-harvest stage.

16.3.7 Oxygen and Carbon Dioxide

Aerobic organisms such as green plants require oxygen to absorb ions (Mengel and Kirkby, 1978). In a study of overall growth response of *N. tobaccum* var. Maryland Mammoth (tobacco), *L. esculentum* var. Marglobe (tomato), and *Soja max* var. Biloxi (soybean) grown from seed with an aerobic root environment, Hopkins et al. (1950) irrigated the plants in 8-mesh quartz sand. In several experiments, they used a modified Shive's four-salt solution with added micronutrients for tomato and soybean and another nutrient solution for tobacco. Mixed gases, consisting of water-saturated N_2 and air combinations over a range between 0.5% and 6.4% O_2, were infused in the sand culture. Forced aeration was used as a control. Hopkins et al. demonstrated that growth response, nutrient accumulation, and nutrient transport all depended upon oxygen supply in the root zone. Root growth of all plants stopped at an oxygen content of 0.5% O_2 in the gas around the roots, although top growth and ion accumulation continued at this level. In tomato, growth and ion accumulation were proportional to log pO_2 from 0.5% to 21% O_2. It was shown that the rate of absorption of phosphate increased from 0 to about 3 mol P × 10^{-7} g^{-1} root h^{-1} as the oxygen tension was increased from 0 to about 2.4% (Hopkins, 1956). The study of Hopkins (1956) is but one example of the necessity of oxygen for active uptake of an essential nutrient across cell membranes.

The mechanism for NO_3^- uptake into barley (*H. vulgare* L.) plants was investigated, and the net uptake rate of NO_3^- by barley plants, which had previously received little nitrogen, decreased from approximately 2 μmol NO_3^- g^{-1} min^{-1} to slightly more than zero μmol NO_3^- g^{-1} min^{-1} after 14 min of exposure. During the same period, the accumulation of NO_3^- increased from 0.4 μmol NO_3^- g^{-1} min^{-1} to about 2.0 μmol NO_3^- g^{-1} min^{-1}, which was explained by Deane-Drummond (1984) as being due to loss of NO_3^- from the cells by "facilitated diffusion."

Copper is an element that is preferentially absorbed through thylakoid membranes. The internal volume of thylakoid membranes was determined to be about 3.3 μL mg^{-1} chlorophyll (Heldt et al., 1973). Assuming a protein to chlorophyll ratio of 4: 1 for thylakoid membranes, the calculated initial rate of Cu^+ transport is approximately 70 pmol min^{-1} mg $protein^{-1}$. By comparison, Fe^{2+}, Cd^+, and Mn^{2+} were slowly transported across the thylakoid membranes, giving initial rates of transport of 5.0 and 2.0 pmol min^{-1} mg $protein^{-1}$, respectively. Mn^{2+} transport was negligible (Shingles et al., 2004).

Effects of imposing oxygen stress, or hypoxia, in the root zone upon nutrient and water absorption of roses and chrysanthemums were investigated by Flannery (2008). There was no apparent relationship between the rate of NO_3^- absorption within the range of –100 to about 320 μg NO_3^- g of rose $plant^{-1}$ d^{-1} and rootzone dissolved oxygen concentration from 2 to 8.4 mg L^{-1} of nutrient solution. Moreover, no relationship was evident between NO_3^- absorption within the range of approximately –120 to 600 μg NO_3^- ml of rose $root^{-1}$ d^{-1} and rootzone dissolved O_2 concentration from 2 to 8.4 mg L^{-1} of nutrient solution.

Within a range of rates of carbon dioxide assimilation in lettuce (*L. sativa* L.) measured from 1 to 4 mmol gDW^{-1} d^{-1}, Albornoz Gutierrez (2013) used parabolic functions to estimate rates of absorption of Ca^{2+}, Mg^{2+}, and SO_4^{2-} from nutrient solution. The rate of absorption for SO_4^{2-} was positive within a range of CO_2 assimilation rates from about 1 to 4 mmol gDW^{-1} d^{-1}, with the curve having a positive slope over the range of CO_2 assimilation measured. In the same range of values of CO_2 assimilation rate, as the values increased, the values of rate of absorption of Ca^{2+} and Mg^{2+} decreased slightly, reached a minimum near or equal to zero, and then increased to about 120 μmol g Ca^{2+} d^{-1} and about 80 μmol g Mg^{2+} d^{-1}, corresponding to a CO_2 assimilation rate of about 4 mmol gDW^{-1} d^{-1}). Similar trends of increasing rate of absorption of NO_3^-, NH_4^+, $H_2PO_4^-$, and K^+ with increasing rates of assimilation of CO_2 were observed by Albornoz Gutierrez.

Yield increases of eight genotypes of tomato (*L. esculentum* Mill.) grown at ambient CO_2 concentration (about 350 μl CO_2 L^{-1}) and 1000 μl CO_2 L^{-1} were not due to carbon exchange rate (CER, or net photosynthetic rate, mg CO_2 dm^{-2} h^{-1}) increases (Tripp et al., 1991). Yield varied among genotypes, but CER did not. Non-epinastic foliar deformation increased throughout the season, became most severe at elevated CO_2 concentration, and varied among genotypes. Foliar K decreased when deformation severity increased at elevated CO_2 concentration. At 13 weeks and ambient CO_2 level, CER ranged from less than 1 mg CO_2 dm^{-2} h^{-1} in the lower leaves to about 1.5 mg CO_2 dm^{-2} h^{-1} in the middle leaves to about 4 mg CO_2 dm^{-2} h^{-1} in the upper leaves. Treated with 1000 μL CO_2 L^{-1}, at 13 weeks, CER was about 2.0–2.5 μL CO_2 L^{-1} in the lower and middle leaves and about 6 μL CO_2 L^{-1} in the upper leaves. At 19 weeks, CER was between –1.5 and –2.0 μL CO_2 L^{-1} in both lower and middle leaves, regardless of CO_2 treatments, and the CER of the upper leaves was about 1.5 and 3.0 μL CO_2 L^{-1} for the 350 and 1000 μL CO_2 L^{-1} treatments, respectively.

Comparing two partial pressures of CO_2, ambient [35Pa] and ambient plus 35 Pa (70 Pa), on root growth and physiological uptake capacity of loblolly pine (*Pinus taeda* L.) and ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) for 6 months, BassiriRad et al. (1997) found no differences in the fraction of biomass allocated to active fine roots and total N (NH_4^+ + NO_3^-) absorption per unit root dry mass. The elevated CO_2 treatment did, however, result in a significant increase in N acquisition via the roots of loblolly pine, but not of ponderosa pine. During the 6-month experiment, the total N uptake rate of loblolly pine increased significantly ($p \leq 0.01$), from about 5 mg to 7.5 $plant^{-1}$ d^{-1}, and there was a small, but not statistically significant increase of the total N uptake rate of ponderosa pine.

Carbon dioxide moves into leaves through stomata, and the uptake of CO_2 is regulated, in large part, by diffusion (Gaastra, 1959). Immediately outside the stomata in still air, a typical concentration of CO_2 is 4×10^{-4} mg cm^{-3} (corresponding to a volume content of CO_2 of 0.02%) and at the chloroplasts, the concentration of CO_2 may be considered to be zero (Meidner and Mansfield, 1968). Fick's law, $m/t = D\alpha\Delta\rho/l$ where m/t is the mass of the gas in grams diffusing in one second; D is the coefficient of diffusion, α is the cross-sectional area of the path in cm^2; Δρ is the difference in density in g cm^{-3}, and l is the length of the path in cm. The diffusion coefficient is expressed in cm^2 s^{-1}. Meidner and Mansfield have estimated the rates of photosynthetic intake of CO_2 through stomata at 17 mg CO_2 dm^{-2} h^{-1}, and with a wind speed of 5 km h^{-1}, they estimated that CO_2 would move through stomata at a rate of 60 mg CO_2 dm^{-2} h^{-1}. Witjaksono et al. (1999) measured the assimilation of CO_2 by in vitro and exvitro avocado plantlets under conditions of ambient CO_2 concentration and enriched CO_2 concentration. They found that CO_2 assimilation through the stomata was greater (31 ± 7

μmol CO_2 m^{-2} s^{-1}) under ambient CO_2 conditions, whereas enrichment with CO_2 resulted in a lower assimilation rate (17 ± 2 μmol CO_2 m^{-2} s^{-1}). The net photosynthetic rate of pea (*Pisum sativum* L. cv. "Meteor") has been found to be influenced by CO_2 levels in the air. As air-CO_2 level was increased from 100 to 500 ppm, the net photosynthesis rate increased from 10 to 75 μg dm^{-2} min^{-1} (Harvey, 1977).

Measurement of the exchange rates of CO_2 (CER) and O_2 (OER) in roots, leaves, and stems + petioles was used for noninvasive measurement of NO_3^- reduction in the shoots and roots of *Glycine max* L. Merr. cv Maple glen (soybean) plants (Cen and Layzell, 2003). In the presence and absence of 5 mM $^{15}NO_3^-$ in the nutrient solution, CO_2 and O_2 concentrations of plant roots and either leaves or stems + petioles of plants were measured in an open gas exchange system to calculate CER and OER flux data and to calculate the diverted reductant utilization rate (DRUR= 4*[measured rate of CO_2 + measured rate of O_2]) in moles of high-energy electron [e^-] g^{-1} h^{-1}. For the leaves, Cen and Layzell report CER and OER rates for photosynthesis within the range of –16 to +16 μmol m^{-2} s^{-1} and for respiration, rates within the range of –3 to +3 μmol m^{-2} s^{-1} they graphically present leaf DRUR rates within the range of 0 to approximately 25 nmol e^- g^{-1}DW s^{-1}. For stems + petioles, the rates were less, –0.2 to +0.2 μmol g^{-1}DW s^{-1} for CER and OER, and DRUR rates were between 0 and 4 nmol e^- g^{-1}DW s^{-1}.

The movement of dissolved CO_2 and O_2 across the cuticle of the aquatic macrophyte *Vallisneria spiralis* L. was studied by MacFarlane (1992). With no effect of orientation of the cuticle, the isolated cuticular permeabilities were about 2.1 μm s^{-1} for CO_2 and 3.3 μm s^{-1} for O_2. Permeabilities were lower at the leaf base and higher at the apex. As a function of O_2 concentration from about 5 to 120 mmol m^{-3}, dark respiratory O_2 uptake for pieces of expanded *V. spiralis* leaves in artificial pond water at 25°C and pH 6.6 was measured within a range of about 30–190 nmol m^{-2} s^{-1}. MacFarlane (1992) determined that the lipid component of resistance to gas transport appeared to be more permeable to O_2 than CO_2.

16.3.8 Hormones, Enzymes, and Genes

Cytosolic glutamine synthetase (GS1), a key enzyme in the assimilation of NH_4^+ in plants, and high NH_4^+ treatment enhanced the expression of GS1 isogene Gln1;2 encoding a low-affinity high-capacity GS1 protein in Arabidopsis (*Arabidopsis thaliana* L.) shoots (Guan et al., 2016). Root GS activity of a wild type of *A. thaliana* to mutants (1) gln1;1, (2) gln1;2, and (3) gln1;1:gln1;2, grown was compared under standard N (2 mM NH_4NO_3) and high N (10 mM $(NH_4)_2SO_4$) NH_4^+ conditions. Under standard N conditions, root GS activities of the wild type and gln1;1 plants were about 32 μmol h^{-1} g^{-1} fresh weight (FW), whereas the root GS activities of the gln1;2 and gln1;1:gln1:2 plants were about 15 and 14 μmol h^{-1} g^{-1} FW, respectively. A similar pattern of root GS activity was evident for the high N conditions, but root GS activities of the wild type and gln1;1 were about 20 μmol h^{-1} g^{-1} FW, and the root GS activities of the gln1;2 and gln1;1:gln1:2 plants were about 15 and 13 μmol h^{-1} g^{-1} FW, respectively.

Mobilization of phosphate between source and sink organs of *A. thaliana* is influenced by the inorganic phosphate (P_i) transporter Pht1;5, implicated in mobilizing stored P_i out of older leaves (Nagarajan et al., 2011). Overexpression of Pht1;5 resulted in altered Pi remobilization, based on evidence of a greater than twofold increase in the accumulation of P_i in siliques, premature senescence, and an increase in transcript levels of genes involved in P_i scavenging. The Pht1;5 overexpressors exhibited increased root hair formation and reduced primary root growth. The study also provided evidence for a link between P_i and ethylene signaling pathways. The uptake rates of 33 pmol P_i g^{-1} FW^{-1} h^{-1} in the roots are provided for the wild type and three mutants of the pht gene. Detailed information regarding the Pht1;5 gene is provided by the National Center for Biotechnology Information (2019).

In a field experiment of N uptake by a sorghum (*Sorghum bicolor* (L.) Moench cv CSH 9) and a local variety (*S. bicolor* cv. FSRP), relative absorption rate of N (RAR, μg N g^{-1} d^{-1}) in the whole plant, specific root absorption rate of N per root weight (SAR, μg N g^{-1} d^{-1}), and specific root absorption rate of N per root length (SARL, μg N m^{-1} d^{-1}) at physiological maturity were measured. RAR, SAR, and SARL were higher for the hybrid CSH9 than for the local variety FRSP with 0 N or 100 kg N ha^{-1} (100 N) fertilizer treatment; the differences between genotypes were significant (P = 0.05) for the 0 N treatment, but were not significant for the 100 N treatment. N absorption was regulated by root activity, that is, by specific N absorption rate per unit root mass and length (Nakamura et al., 2002).

In a study of leaves of maize (*Z. mays* L.) focusing on the relative intercellular distribution of NO_3^--assimilating and NADH-generating enzymes and the relationship between the photosynthetic C-4 pathway and NO_3^- assimilation, Neyra and Hageman (1978) determined that the mesophyll cells are the major site for NO_3^- assimilation in the leave blade. Nitrate reductase (NR), nitrite reductase (NiR), and the NO_3^- content of leaf blades were localized primarily in the mesophyll cells, but some NiR was found in bundle sheath cells. Because the specific activity of NR was sevenfold lower than the that of the other enzymes involved in NO_3^- assimilation, NO_3^- reduction was indicated as the rate-limiting stem in situ. NR activity in

fractions isolated from the leaves of maize seedlings were 1.34 and 0.07 μmol NO_2^- produced h^{-1} mg^{-1} protein in the mesophyll and bundle sheath, respectively. NiR activity in fractions isolated from the leaves of maize seedlings were 9.4 and 2.10 μmol NO_2 reduced h^{-1} mg^{-1} protein in the mesophyll and bundle sheath, respectively.

The roles of the outward Shaker K^+ channel gene OsK5.2 in controlling stomatal movements and K^+ loading into xylem sap of *A. thaliana* were investigated by Nguyen et al. (2017). Expression of the OsK5.2 gene was observed in the entire stomatal complex (guard cells and subsidiary cells), as well as in the root vasculature and root cortex. Loss of OsK5.2 functional expression in stomata resulted in a severe slowdown of stomatal closure and higher rates of water loss through transpiration, as well as lack of time-dependent outward potassium currents in guard cells. Mutant plants in which OsK5.2 was not expressed displayed reduced K^+ translocation from the root system toward the leaves via the xylem.

Five cultivars of cherry tomato [*Solanum lycopersicum* L. (*Lycopersicon esculentum* Mill.)] were germinated from seed and grown in a tray with wells. Next, the cultivars (Kosaco, Josefina, Katalina, Salomé, and Zarina) were transferred to a cultivation chamber under controlled photoperiod, temperature, relative humidity, and photosynthetic photon-flux density where they were grown in pots with 1:1 peat:vermiculite mixture and a complete nutrient solution. Water-stress treatments with 50% of field capacity (FC) was used, with 100% FC control. There was a general decrease in growth, and there were lower concentrations and uptake of macronutrients and micronutrients in four of the five cultivars. The Zarina cultivar displayed better growth and increased concentrations and uptake of N, P, Mg, K, and Cl, compared to the control plants. Tables of uptake fluxes (mg $plant^{-1}$ d^{-1}) of macronutrients and micronutrients are presented by Sánchez-Rodríguez et al. (2010).

16.3.9 Nanoparticles

Nanoparticles are increasingly used in agriculture, feed, and food (Peters et al., 2014). In experiments with whole tobacco plants treated with various concentrations of 5, 10 or 20 nm nanoparticles of iron oxide [(Fe_3O_4) NPs], Alkhatib et al. (2014) observed drastically reduced photosynthetic rate and leaf area in plants treated with 5 nm (Fe_3O_4) NPs, compared to control plants and plants treated with 10 or 20 nm (Fe_3O_4) NPs. Alkhatib et al. also found that protein concentration in plants treated with 5 nm (Fe_3O_4) NPs increased, compared to control plants. They concluded that 5 nm (Fe_3O_4) NPs were highly toxic, because of these findings and the fact that tobacco plants treated with 5 nm (Fe_3O_4) NPs showed deformed epidermal cells, thickened cell walls in vascular tissues (mainly the xylem), and reduced number of cortical cell layers. The experimental data also showed that 5, 10, and 20 nm (Fe_3O_4) NPs reduced transpiration rate to about 1 mmol (H_2O) m^{-2} s^{-1}, compared to about 2.5 mmol (H_2O) m^{-2} s^{-1} of the control, and stomatal conductance was reduced to about 20 mol m^{-2} s^{-1} in plants treated with 5, 10 or 30 nm (Fe_3O_4) NPs, compared to 90 mol m^{-2} s^{-1} of the control.

In an in vivo study of Zn transport and time-dependent physiological effects of zinc sulfate ($ZnSO_4$) and zinc oxide (ZnO) nanoparticles of 40- and 300-nm diameter, Da Cruz et al. (2019) found that 40-nm particles of ZnO were more easily dissolved than were 300-nm particles of ZnO. Zinc transport velocity (10^{-7} counts h^{-1}) was measured at three points of the stem and petiole of *P. vulgaris* L. (bean) whose roots were exposed to 100 mg Zn L^{-1} for three treatments $ZnSO_4$ (aq), 40 nm ZnO and 300 nm ZnO. Velocities of Zn translocation measured along the stem and petiole were highest for $ZnSO_4$, decreasing from 4×10^{-7} counts h^{-1} at P1 to about 2×10^{-7} counts h^{-1} at P2 to P3 to the petiole. A similar pattern of translocation velocity of Zn was evident for the 40 nm ZnO nanoparticle suspension, but translocation velocity at each point was less for the 40 nm ZnO nanoparticles than it was for the dissolved $ZnSO_4$. The slowest velocity of Zn translocation at P1, about 30×10^{-7} counts h^{-1}, was for the 300 nm ZnO nanoparticle treatment, and Zn translocation velocity for this treatment was measured as being essentially nil at points P2, P3, and the petiole. Similar patterns of transport velocity, but with different values of the velocity of Zn transport in the xylem were measured by exposing the roots to 1000 mg Zn L^{-1} utilizing the three Zn treatments used when exposing the roots to 100 mg Zn L^{-1}.

Nano-silver (NS) is a strong antibacterial agent. Lin et al. (2019) found that pretreatment with NS at 10, 15, 20, 25, or 30 mg L^{-1} for 24 h significantly extended the life of cut gardenias (*Gardenia jasminoides* Ellis var. "fortuniana"). The most effective NS concentration, 15 mg L^{-1}, resulted in the longest vase life extension, 15.2 d, which was 310% of the life of the control treatment which water to which no NS was added. Scanning electron microscopy showed higher water balance values and higher relative fresh weight when NS was present in the water, resulting from improved water uptake as a result of alleviation of bacterial xylem blockage at the stem ends. From day 1 through day 9, water uptake with 15 mg L^{-1} NS increased from about 10 to 17 g $stem^{-1}$ d^{-1} on day 3 and then declined to 9 g $stem^{-1}$ d^{-1} on day 9. In a marked contrast, without NS, water uptake decreased from about 9 g $stem^{-1}$ d^{-1} on day 1 to 1 g $stem^{-1}$ d^{-1} on day 4.

A study was conducted by Rossi et al. (2019) to determine effects of foliar Zn fertilization of coffee (*Coffea arabica* L.) plants, comparing two Zn treatments of

equal Zn concentration, that is, zinc sulfate monohydrate ($ZnSO_4 \cdot H_2O$) and zinc oxide fertilizer nanoparticles (ZnO NPs), to an untreated control. The average diameter of the zinc nanoparticles used is 68.14 nm, and the range of diameter of the nanoparticles used is 15–137 nm. ZnO NPs aggregated in liquid solution; the average hydrodynamic size of ZnO NPs in 100 mg L^{-1} of the solution was measured as 621 nm by dynamic light scattering (DLS) method. One-year-old coffee plants grown in greenhouse conditions were treated with two foliar applications of 10 mg L^{-1} of Zn as either $ZnSO_4 \cdot H_2O$ or ZnO NPs. Compared to the control, the ZnO NPs increased the fresh weight (FW) of the roots by 37% and FW of the leaves by 95%. Compared to the control, the ZnO NPs increased the DW of the roots, stems, and leaves by 28%, 85%, and 20%, respectively. Net carbon assimilation rate measured from 0 to 30 d after sowing (DAS) was constant for the ZnO treatment, about 6 μmol m^{-2} s^{-1}, but increased at 40 DAS. During the same period, the net carbon assimilation rate of the control plants was within the range of 4 to 6 μmol m^{-2} s^{-1} and the net carbon assimilation rate of the $ZnSO_4 \cdot H_2O$ treatment ranged between 4 and 8 μmol m^{-2} s^{-1}.

16.3.10 Mycorrhizal Fungi

The role of arginine (Arg) in translocation of N by *Rhizophagus irregularis*, also known as *Glomus intraradices*, an arbuscular mycorrhizal (AM) fungus associated with the roots of carrot (*Daucus carota* L.) was studied by Cruz et al. (2007). Measuring rates (μmol mg $protein^{-1}$ h^{-1}) of the enzymes glutamine synthetase (GS), argininosuccinate synthetase (ASS), arginase, and urease, they concluded that the catabolic activity of the urea cycle in the roots depends upon translocation of Arg from the extraradical mycelium (ERM). Using ^{15}N-labeled Arg in the ERM, the translocation rate of Arg along the mycelium was estimated to be 0.13 μg Arg mg^{-1} fresh weight h^{-1}.

Dual symbiosis between arbuscular mycorrhiza (AM) and nitrogen-fixing bacteria (NFB) was shown by Mortimer et al. (2013) to dramatically increase uptake rates of N and P by a woody invasive legume, *Acacia cyclops* A. Cunn ex G. Don, under nutrient-limiting conditions. Four combinations using neither naturally occurring NFB and the AM *Glomus mossea*, either separately, or both to inoculate *A. cyclops* provided plants that were cultivated in sand and supplied with a 20% strength nutrient solution. Although dual inoculation decreased the colonization of both symbionts, compared to a single symbiosis with either symbiont, N and P acquisition and utilization were greatly increased by the dual inoculation. For example, the P absorption rate almost nil with no inoculation or inoculation with only NFB, was about 0.025 mg P g^{-1} root DW d^{-1} with inoculation by AM, and was 0.17 mg P g^{-1} root DW d^{-1} with inoculation by both NFB and AM. The N absorption rate was about 0.1 mg N g^{-1} root DW d^{-1} with no inoculation, inoculation with only NFB, or inoculation with only AM, but was about 0.8 mg N g^{-1} root DW d^{-1} with both NFB and AM inoculation.

In a study of effects of mycorrhiza on N metabolism in durum wheat (*Triticum durum* Desf.) under a range of P fertilization rates, Di Martino et al. (2018) found that the specific nitrate reductase activity (NRA) in the roots and leaves was greater in plants with mycorrhiza than in plants without mycorrhiza. The NRA in the roots was significantly greater, 30, 29, and 27 mmol min^{-1} mg^{-1} protein (prot.) for 7, 15 and 25 μg P g^{-1} soil DW, compared to 10, 16, and 21 mmol min^{-1} mg^{-1} prot. without mycorrhiza at 7, 15, and 25 μg P g^{-1} soil DW. At these three lower P concentrations of soil P, the plants having roots with mycorrhizae displayed a greater capacity to reduce NO_3^- and a greater capacity to assimilate NH_4^+ in the leaves, compared to the plants without mycorrhizae. NRA in the roots of plants treated with 45 μg P g^{-1} soil DW was not significantly different ($P \leq 0.05$) 56 d after sowing (DAS), about 25 mmol min^{-1} mg^{-1} prot., with or without mycorrhiza. Similarly, in the leaves, when treated with 25 or 45 μg P g^{-1} soil DW, the NRA was approximately 25 nmol min^{-1} prot. Greater glutamine synthetase activity in the leaves of the mycorrhizal wheat plants at 7, 15, and 25 μg P g^{-1} soil DW, compared to the non-mycorrhizal plants, indicates enhanced ability to assimilate NH_4^+. The mycorrhizal plants presented a chloroplastic isoform that could function as a sink to reduce oxidizing NADPH to NADP. The mycorrhizal wheat plants included the highest concentrations of P, K, Ca, N, Fe, Zn, and Mn, as well as free amino acids, protein, NAD, NADP, AMP, ADP, and ATP in the roots and leaves. Mycorrhizal colonization of the wheat roots was inversely related to soil P content.

Uptake of NO_3^- by tomato plants growing in P-deficient soil was increased by the mycorrhizal fungus, *G. mosseae* (Di Martino et al., 2019). At the stage of harvesting fruit, plants with mycorrhiza had significantly higher concentrations of mineral nutrients and nitrogenous organic compounds. Compared to non-mycorrhizal plants, plants with mycorrhiza contained about 35% more glutamic acid (GLU), glutamine (GLN), aspartic acid (ASP), and asparagine (ASN). Nitrate reductase specific activity (nmol min^{-1} mg^{-1} prot.) and glutamine synthetase activity (nmol min^{-1} mg^{-1} prot.) were also greater in the mycorrhizal tomato plants, compared to those lacking mycorrhiza. Fruit yield of the mycorrhizal plants was approximately 50% greater than that of the non-mycorrhizal plants, and fruit began to develop and became ripe earlier in the mycorrhizal plants compared to the non-mycorrhizal plants.

To assess the influence of mycorrhizal inoculation and different grafting methods of salt-stressed cucumber seedlings regarding plant establishment and nutrient absorption rates, Sallaku et al. (2019) grafted young cucumber (*Cucumis sativus* L.) plants onto arbuscular-mycorrhizal-fungi (AMF)-free or AMF-inoculated *Cucurbita maxima* × *Cucurbita moschata* transplants by two grafting methods, that is, common root intact, splice grafting (SG), and root-pruned splice grafting (RPSG). Self-rooted plants were kept as control. AMF inoculation that significantly increased relative growth rate of the plant (RGR_{plant}, g g^{-1} d^{-1}) was strongly correlated (ANOVA, $p <$ 0.01) in all three grafting types and under both saline and non-saline conditions. In addition, AMF inoculation significantly (ANOVA, $p < 0.05$–0.001) influenced the specific absorption rate (SAR, mg g^{-1} d^{-1}) of Al, Ca, Fe, K, Mg, Na, P, and S.

Mycorrhizal associations with plant roots have been shown to increase uptake of phosphate by roots of onion plants. Sanders and Tinker (1973) showed that during 14 days, the rate of mycorrhizal phosphate uptake by the roots of onion plants was 0.17 pmol cm^{-1} s^{-1}, compared to non-mycorrhizal uptake which was 0.050 pmol cm^{-1} s^{-1}. Similarly, during a 10-day experiment, they found that the rate of mycorrhizal phosphate uptake by the roots of onion plants was 0.13 pmol cm^{-1} s^{-1} compared to non-mycorrhizal uptake which was 0.042 pmol cm^{-1} s^{-1}. Eight-day-old maize (*Z. mays* L.) seedlings replete with nitrogen, when placed in N-deficient solutions, increased their rate of absorption of NO_3^- and NH_4^+ uptake from 200 μM NH_4NO_3. Patterns of uptake changed during a 72-h period. During the 72 h of exposure, the rate of uptake of NH_4^+ increased from about 5 to 9 μmol g^{-1} h^{-1}, whereas the rate of uptake of NO_3^- increased from 2 to 5 μmol g^{-1} h^{-1}, then declining to about 4 μmol g^{-1} h^{-1}. More detailed rate data for shorter periods of time during the 72 h are also included in the report by Jackson and Volk (1992).

16.3.11 Rates of Transport of Essential Plant Nutrients in the Vascular System

Long-distance transport in the xylem and phloem is described in a review by White (2012b), including the anatomy of xylem and phloem, the composition of xylem and phloem saps, movement of xylem sap from root to shoot, and movement of phloem sap. He includes topics such as water-potential gradients, source/sink relationships, pathways of solute movement within the plant, and transport proteins that catalyze loading and unloading of elements to and from the xylem and phloem.

Peel (1974) provides an insightful discussion of the measurement and concepts of velocity and mass transfer of solutes in the vascular systems of plants. At the outset, he states that volume transfer (cm^3 h^{-1}) = area (cm^2) × velocity (cm h^{-1}), and to calculate mass transfer: mass transfer (g h^{-1}) = volume transfer (cm^3 h^{-1}) × concentration (g cm^{-3}) or specific mass transfer (g cm^{-2} h^{-1}) = velocity (cm h^{-1}) × concentration (g cm^{-3}).

Effects of drought were induced by Cai et al. (2019), using to study K^+ uptake in the roots and translocation from root to shoot in six genotypes of *H. vulgare* L. (barley). Ion flux measurements were achieved using microelectrode ion flux estimation (MIFE) system and 3-day-old seedlings with 7- to 8-cm-long barley roots. Polyethylene glycol (PEG8000) was added to the aerated basic salt medium (BSM) used as the control condition to create an osmotic environment simulating an osmotic effect of drought in the BSM rooting medium. Net K^+ flux during the 60-min experimental period ranged between 0 and 500 nmol m^{-2} s^{-1}, and the flux patterns differed among three pairs of barley genotypes, that is, WMLL and XZ141, Morex and XZ5, and Gairdner and XZ147.

External factors such as soil moisture content and vapor pressure deficit and internal factors such as source/sink phenomena are cited by Gourieroux et al. (2016) to explain changes in rates of transport of amino acids in the xylem and phloem of petioles of leaves and rachises of bunches of berries of *Vitis vinifera* L. "Cabernet Sauvignon." Seasonal and diurnal fluctuations in the amino acid exudation rate of rachis and petiole were measured, in μmol h^{-1}. Amino acid exudation rate in the rachis during season 1 reached a maximum of about 0.5 μmol h^{-1}, whereas the corresponding maximum rate in season 2 was only about 0.014 μmol h^{-1}. Amino acid exudation rates from the petioles were much lower, reaching a maximum of about 0.8 μmol h^{-1} in season 1 and about 0.004 μmol h^{-1} in season 2. At each of the seven samplings every 4 h during the 24-h day, amino acid exudation rates of the rachis were consistently greater pre-veraison, compared to post-veraison. In five of the seven samplings every 4 h during the 24-h day, amino acid exudation rates of the petiole were consistently greater pre-veraison, compared to post-veraison.

16.3.11.1 Xylem

The xylem of vascular plants is specialized tissue that conducts solutes from the root to shoot; it can be considered a continuous system of interconnected tubes with little resistance to the flow of water but also includes living parenchyma cells which are involved with loading solutes into the xylem (Shabala, 2007). Dead, lignified cells called vessels and tracheids transport solutes and water, and xylem flow rates are about 13 mm s^{-1} in trees with large vessels (Taiz and Zeiger, 1991). Flow rates of water and solutes in wheat have been measured at a mean speed of 0.8 mm s^{-1} (Passioura, 1988).

The rate of P_i movement in xylem vessels has been measured at about 200 cm h^{-1}, and phosphorus redistribution in vascular plants has been found to be very rapid, the transport of P_i in the phloem occurring at a rate of about 50 cm h^{-1} (Kolek and Kozinka, 1992). In maize plant xylem, 79–82% of the total activity of ^{32}P-compounds transported in xylem exudate was P_i, 3–7% was the fraction of phosphoric acid esters of glycides, and 13–17% was free nucleotides (Michalík and Ivanko, 1971).

Root pressure exudation experiments of Anderson (1975) entail cleanly cutting the stem of a root system and measuring the volume and chemical composition of the xylem sap at various points in time. From the primary experimental data of the rate of xylem exudate production and the concentration of any ion in the xylem sap, the ion flux through the xylem may be calculated as $J_s = J_v \cdot C_s$ where J_v is the exudation volume flux normalized over unit area of root surface or over unit fresh weight of root for highly branched root systems, and C_s is the concentration of the ion *s* in the exuded xylem sap. J_s is the ion flux emerging at the cut end of the root. Values of J_s reported by different investigators for K^+, Cl^-, SO_4^{2-}, NO_3^- in xylem exudates of *Z. mays, R. communis, Sinapsis alba, Triticum aestivum, Avena fatua, Avena sativa, H. annuus*, and *Allium cepa* are organized in a tabular format by Anderson (1975).

Eichert and Goldbach (2010) investigated the effects of varying relative humidity (RH) on the mobility of B in xylem and phloem of intact seedlings of *R. communis* L. cv. Impala (castor bean). They found that at 30% and 70% RH, there were no significant differences in the rate of B flow in the xylem 21 h after foliar application of 10 mM boric acid [$B(OH)_3$] for 30 min to seedlings and seedlings of the untreated control. However, they did find that at 100% RH, the B flow rate in the xylem of the treated plants was about 2 μg B h^{-1}, compared to about 0.5 μg B h^{-1} of plants of the untreated control, a significant difference ($P < 0.05$) that they attribute to foliar-applied B being transported to the roots but then being returned to the xylem since, they explain, under conditions of water saturation of ambient air, root pressure often replaces transpiration as a driving force of xylem flow (Pickard, 2003).

Features such as size, number, and total vessel area were found by Fassio et al. (2009) to affect the sap flow rate in xylem vessels of "Hass" avocado (*Persea americana* Mill.) trees. Comparing trees composed of "Hass" scions and two clonal rootstocks as well of trees of Duke 7 and Toro Canyon varieties, the sap flow rate was 29% greater for clonal Duke 7 (D7) trees, compared to Toro Canyon (TC) trees. Although there were no differences among xylem vessel features in the stems of any of the varieties, in the roots, D7 trees had wider and fewer vessels than did TC trees. Sap flow ranged between about 10 g $tree^{-1}$ h^{-1} at 0800 hrs (8:00 a.m.) to a maximum of about 90 g $tree^{-1}$ h^{-1} of ungrafted D7 trees and a maximum of about 60 g $tree^{-1}$ h^{-1} of trees of "Hass" scions grafted on Duke rootstock (H/D7). The sap flow rate of D7 declined from about 90 g $tree^{-1}$ h^{-1} at 1600 hrs to < 10 g $tree^{-1}$ h^{-1} at 2000 hrs, and the sap flow rate of H/D7 declined from about 60 g $tree^{-1}$ h^{-1} to < 10 g $tree^{-1}$ h^{-1} at 2000 hrs. Light micrographs and additional data regarding sap flow rates are presented by the authors for TC trees and trees of "Hass" scions grafted on TC rootstock (H/TC).

Mobilization and transport of N and C via xylem sap toward new shoots of the shrub *Ligustrum ovalifolium* (privet) was studied from bud break (Guérin et al., 2007) by (1) speciation of soluble N and C forms in xylem sap and (2) estimation of kinetics of N and C fluxes in xylem sap during spring growth of the shoots. *L. ovalifolium* shrubs were grown for 2 years with or without fertilization in the second spring. Glutamine was the principal form of amino-N at bud break and during shoot elongation. However, in fertilized plants, arginine became predominant after shoot elongation and was related to low C availability. At the beginning of stem elongation, xylem sap mean flow rate in the fertilized plants was 15 ml $plant^{-1}$ d^{-1}. In unfertilized plants, xylem sap mean flow rate at the beginning of stem elongation was about three times higher, that is, 49 ml $plant^{-1}$ d^{-1}.

Using $H_2{}^{15}O$ and gamma ray detectors, Ohya et al. (2008) detected a large volume of water escaping from the xylem vessels in the stem of soybean [*G. max* (L.) Merr. Cv. Enrei] grown in 1/5 Steinberg solution. The transpiration rate declined from about 0.018 to 0.006 g water cm^{-2} h^{-1} as relative humidity increased from 30% to about 95%. The escape of water from the xylem was not influenced by evaporation from the stem surface or mass flow in the sieve tubes, and most of the water that escaped from the xylem reentered the xylem vessels. Analysis using a mathematical model showed that the net volume of water that escaped from xylem vessels was not dependent upon the transpiration rate of the plant.

Using plants of *Brassica napus* L. *cv*. Capitol (oilseed rape) that had previously been treated with a nutritionally sufficient nutrient solution that included 1 mM KNO_3, Orieux et al. (2018) determined that a subsequent, high external NO_3^- concentration (5 mM KNO_3) increased water uptake by the roots. They also found that NO_3^- translocation depended upon both the rate of NO_3^- uptake by the roots and loading into the xylem. Water uptake and transpiration of *B. napus* plants treated with 0.5 mM KNO_3 with high transpiration (HT) at 65% relative humidity (RH) increased from 0 at midnight (0 h) to between 40 and 50 g h^{-1}) from 7 to 11 h, declining to between 0 and 15 g h^{-1} at night. With the same KNO_3 treatment, water

uptake and transpiration rates of *B. napus* plants with low transpiration (100% RH) were mainly between 0 and 20 g h^{-1}. Treated with 5 mM KNO_3 and high transpiration (65% RH), water uptake and transpiration rates reached as high as 50–60 g h^{-1} during the period, 7–11 h, declining to between about 5 and 20 g h^{-1} at night. With the same high KNO_3 treatment and low transpiration (100% RH), water uptake and transpiration rates of *B. napus* plants were mainly between –10 and 150 g h^{-1}. The mean 5/0.5 ratio of NO_3^- mass flow for the high- and low-N treatments was significantly ($P < 0.005$) greater (about 18 µmol h^{-1} cm^{-1} root/ µmol h^{-1} cm^{-1} root) with high transpiration than with low transpiration (about 12 µmol h^{-1} cm^{-1} root/µmol h^{-1} cm^{-1} root).

Diurnal variations in the xylem sap composition and measurements of xylem sap flow rates of poplar (*Populus tremula* × *Populus alba*) show that the maximum translocation rate (mmol h^{-1} g^{-1} FW total) for six macronutrient ions (NO_3^-, $H_2PO_4^-$, SO_4^{2-}, K^+, Mg^{2+}, and Ca^{2+}) occurred during the first half of the illumination period (1000 hrs) and decreased by 40–53% (depending upon the ionic species) at the end of the light period (Siebrecht et al., 2003). In contrast, the maximum sap flow rate (ml h^{-1} g^{-1} FW) was observed later (1600 hrs) and dropped by 22% at the end of the light period, indicating that the translocation of ions via the xylem into the shoot is regulated not exclusively by the flow of xylem sap, which depends on the transpiration stream, but also by the process of xylem loading that could be regulated by nutrient demand of the shoot. During the night translocation of ions to the shoot continued, but translocation rates were 63–69% lower, depending upon ion species, compared to the maximum translocation rate of each ionic species in the light.

16.3.11.2 Phloem

Sieve tubes of the phloem carry both organic compounds synthesized in the leaves and inorganic ions. Zimmerman (1969) measured rates of movement of a mixture of stachyose, raffinose, sucrose and D-mannitol in the sieve tubes of American ash to range between 30 and 70 cm h^{-1}. Using radiotracer methods and employing two colonies of aphids to remove honeydew samples, Peel and Weatherley (1962) found the rate of movement of the phloem to have been between 25 and 33 cm h^{-1}. Using a thermoelectric technique on exposed phloem tissue of a species of *Heracleum*, Ziegler and Vieweg (1961) measured the movement of solutes in the phloem within a range of velocity from 37 to 70 cm h^{-1}. Canny (1960) has reported mass transfer rates in the phloem of various plant species with a range from 0.14 to 4.8 g DW cm^{-2} phloem h^{-1}.

In the phloem, rates of transport of different substances have been measured. Radioactive phosphorus, when injected into cotton leaves, was found to be phloem-mobile, with downward rates of translocation greater than 21 cm h^{-1} (Biddulph and Markle, 1944). Applying $^{14}CO_2$, tritiated water ^3H_2O, and ^{32}P-labeled inorganic phosphate to leaves of red kidney bean plants, Biddulph and Cory (1957) found that after 15 min migration time, the tracers moved at different rates: ^{32}P at 86.5 cm h^{-1}; ^3HHO at 86.5 cm h^{-1}, and ^{14}C at 107 cm h^{-1}. Subsequent research with excised strands of *Heracleum* phloem injected with [^{14}C]sucrose and ^{42}K into a single sieve element showed after 2 min that ^{14}C traveled at about 200–500 cm h^{-1} and ^{42}K traveled at 30–60 cm h^{-1} (Fensom, 1972).

Plant hormones, as defined by a Committee of the American Society of Plant Physiologists in 1954, "are regulators produced by plants, which in low concentrations regulate plant physiological processes. Hormones usually move within the plant from a site of production to a site of action" (American Society of Plant Physiologists, 1954). Plant hormones and inorganic nutrients are both factors that influence the growth and development of plants, since hormones internally regulate growth and inorganic nutrients meet the essential requirements of the plant by maintaining the osmotic potential of the cells and tissues and by serving as components of organic compounds and cofactors in biological reactions (Karmoker, 1985). Auxin is a generic term for plant hormones that induce elongation in the shoot cells, and they resemble indole-3-acetic acid (IAA) in their physiological action (Marumo, 1986). Auxins move in a basipetal direction that is away from meristematic tissue. The rate of movement of IAA in short tissue sections has been measured within a range of 5.7–15 mm h^{-1} in tissues such as *Phaseolus* epicotyl, *Zea* coleoptile, *Zea* root, and *Avena* coleoptile (Goldsmith, 1968).

The rate at which sugar is translocated in the phloem is directly related to the net photosynthesis rate. Servaites and Geiger (1974) demonstrated a linear relationship between the rate at which ^{14}C was translocated via the phloem from the leaves of 19 sugar beet plants and the net rate of photosynthesis. Translocation rates of ^{14}C in the phloem, which they measured, range from approximately 5 µg C dm^{-2} min^{-1} to 50 µg C dm^{-2} min^{-1} for a range of net photosynthesis rate from 0 to approximately 260 µg C dm^{-2} min^{-1}. This research supports the hypothesis that the mass transfer rate of translocation of sugars from the leaves under conditions of sufficient sink demand is limited by the net photosynthesis rate or more specifically by the rate of synthesis of sucrose, and that this limitation is independent of light intensity per se.

Phloem carbon translocation from the canopy to below-ground sinks of a hinoki cypress (*Chamaecyparis obtuse* (Siebold & Zucc.) Endl.) stand of 155 trees was found to be related to stem diameter (cm) measured at 1.3 m height (Epron et al., 2018). For the stand, the computed

hydraulic conductance was 1.7×10^{-15} mPa^{-1} s^{-1}, the estimated rate of carbon translocation of 2.0 g C m^{-2} d^{-1}, or 1.8 g C m^{-2} d^{-1} if the two biggest trees were discarded. As a function of a range of stem diameter from about 5 to 40 cm (excluding two trees with stem diameter of about 55 cm) at 1.3 m height, for the phloem, conductivity increased within a range of increasing values from about 0 to 6×10^{-13}, m^4 Pa^{-1} s^{-1}, conductance increased within a range of about 2 to 3.3×10^{-14}, m^4 Pa^{-1} s^{-1}, and the rate of translocation of carbon was calculated to increase within the range of about 1 to 50 g C d^{-1}.

A heat balance method combined with girdling, which cuts off phloem, of eight-year-old Meiwa kumquat (*Fortunella crassifolia* Swingle) citrus trees was used to measure sap flow rates of phloem and xylem (Nakano and Iwasaki, 2019). Using these techniques in non-bearing branches, they measured phloem sap rates of –0.12, –0.27, and –0.28 g h^{-1} on three separate days in November 2010, the negative values indicating basipetal flow. Corresponding xylem sap flow rates on the three days are 1.99, 10.9, and 2.74 g h^{-1}, positive values indicating acropetal flow. On three other days in November 2010, in bearing branches, Nakano and Iwasaki measured phloem sap rates of 0.48, 0.37, and 0.30 g h^{-1}, and all the values were positive, indicating acropetal flow. Corresponding xylem sap flow rates for the bearing branches on the same three days are 1.03, 2.63, and 2.53 g h^{-1}, and the positive values indicate acropetal flow. These investigators determined that phloem sap flowed basipetally in the non-bearing type of branch and acropetally toward the fruits in the bearing type of branch.

16.3.12 Reproductive Organs (e.g., Flowers, Fruit, Seeds) and Storage Organs (e.g., Tubers)

During the development of the fruit of *Prunus avium* L., "Sam" (sweet cherry), flow in the phloem into the fruit increased, eventually accounting for 100% of the sap influx to the fruit, while xylem flow decreased, eventually reaching zero (Brüggenwirth et al., 2016). As a result, fruit water potential became independent of the tree once the fruit was mature. Measurements to calculate flows of transpiration (F_{trans}), xylem (F_{xylem}), and phloem (F_{phloem}) were taken periodically from 19 to 76 days after full bloom (DAFB) in trees irrigated with a drip system. Flows of transpiration ranged from approximately –0.6 to 0 ml d^{-1} per fruit, whereas flows of xylem and phloem were mainly positive, within the range of slightly less than 0 to 0.4 ml d^{-1} per fruit. The study includes a graphical presentation of data showing representative diurnal time courses of xylem, phloem, and transpiration flows (μL h^{-1} per fruit) of the sweet cherry fruit within the range of solar time from 8:00 a.m. of each day to 8:00 a.m. of the subsequent day.

In another study of the diminishing role of xylem in the filling of fleshy fruit, Choat et al. (2009) measured xylem hydraulic resistance (R_h) in the developing fruit of grape (*V. vinifera* "Chardonnay") 20–100 d after anthesis (DAA) and compared their measurements with observations of microscopic xylem anatomy and expression of six plasma membrane intrinsic protein (PIP) aquaporin genes. Whole-berry R_h and receptacle R_h increased significantly in the latter stages of ripening (80–100 DAA), associated with deposition of gels or solutes in many receptacle xylem conduits. Basing their graph on data from Greenspan et al. (1996), Choat et al. show backflow from the fruit to the parent plant to decline range from 1000 to less than 200 μL d^{-1} within the range of increasing R_h from 0 to 20×10^{-10} (MPa s m^{-3}). They suggest that the fruit of the grape variety they examined was not hydraulically isolated from the parent plant by xylem occlusion, but that it was "hydraulically buffered" by water delivered by the phloem.

Flowers of Southern magnolia (*Magnolia grandiflora* L.) depend upon long-distance transport to supply water for reproductive mechanisms to function (Feild et al., 2009). Measured at five times, that is, predawn, morning, midday, afternoon, and night, the range of diurnal stomatal conductance for 1st whorl tepals and leaves of the first-day flower was within the range of about 5–230 mmol H_2O m^{-2} s^{-1} and transpiration rate was within the range of 0.1 mmol to about 3 mmol H_2O m^{-2} s^{-1}. At the same diurnal sampling times, the range of the diurnal stomatal conductance of the third whorl of the first-day flower was within the range of about 5–10 mmol H_2O m^{-2} s^{-1} and transpiration rate was within the range of about 0.1 mmol to about 0.2 mmol H_2O m^{-2} s^{-1}.

A potometer and a pressure probe were used to study xylem sap flows in the pedicels of sweet cherry fruit isolated from the tree by a cut at the proximal end of the fruit + pedicel (Winkler et al., 2016). The results of their experimentation indicate that pedicel xylem flow is driven by a gradient in tension caused by osmotic water uptake from the fruit apoplast into the fruit symplast and by transpiration. They also found that the flow of xylem sap decreases toward the maturity of the cherry fruit.

In an experiment, to test the hypothesis that fertilization is an important management strategy of yams (*Dioscorea* spp), Diby et al. (2011) utilized a "full fertilizer" treatment, compared to no fertilization (farmer practice) to measure uptake and calculate nutrient use efficiency of N and K. Rates of fertilizer application were 240 kg N ha^{-1}, 269 kg K ha^{-1}, 11 kg P ha^{-1}, 8.5 kg Ca ha^{-1}, 11 kg Mg ha^{-1}, and 66 kg S ha^{-1}. Regression equations estimating the tuber growth are presented, comparing

growth with and without fertilizer application for two species of yam, *Dioscorea alata* and *Dioscorea rotundata* at forest and savanna sites. For example, the regression equation estimating tuber growth of *D. alata* with no fertilizer at the forest site is y=2.9059 ln(x) – 1.2839 where y = DW of the tuber, x = days after planting, and r = 0.83. This regression equation and others presented by Diby et al. for shoot growth, root growth, and tuber growth are mathematical estimates the mass of the organs of the plant as functions of time. One can use the technique of calculating the first derivative of these regression equations of Diby et al. (2011), utilizing the technique employed by Crawford et al. (1982, 1990), to estimate the net rate of accumulation, or net flux, of the mass of each of the plant organs of the yam plant as a function of time for each species of yam, each fertilizer treatment and each site.

Nitrogen accumulation in plants of the Green Mountain variety of potato (*Solanum tuberosum* L.) began about 20 days after planting (DAP), increased to a maximum of 3.5 lb per acre (ac) d^{-1}, then decreased in a linear manner to a minimum rate of –2 lb ac^{-1} d^{-1} at about 93 DAP after which the rate increased to about –0.2 lb ac^{-1} d^{-1} at 110 DAP (Hawkins, 1946). In the same experiment, measurements of N in the tubers show that N began accumulating in the tubers at 55 DAP, increasing to a maximum rate of accumulation of about 2.4 lb ac^{-1} d^{-1} at about 93 DAP, then decreasing to a rate of 1 lb ac^{-1} d^{-1} at 110 DAP. Measurable amounts of potash (K_2O) began to accumulate in plants of the Green Mountain variety 20 DAP, reaching a maximum rate of accumulation, 6 lb ac^{-1} d^{-1} about 58 DAP, then decreased in an almost linear manner to –4 lb ac^{-1} d^{-1}. Potash began accumulating in the tubers of the Green Mountain variety around 58 DAP – the same day on which maximal accumulation rate of K_2O occurred – and the K_2O accumulation increased to a maximum of about 3 lb ac^{-1} d^{-1} at 90 DAP, after which the rate declined to about 1.4 lb ac^{-1} d^{-1} at 110 DAP.

As a tool for better N management for potato production, Horneck and Rosen (2008) measured the N accumulation rates of vines and tubers of high-yielding irrigated potatoes grown in Minnesota and in Oregon. In addition, they measured the accumulation of dry matter, N, P, K, and Ca (lb/A/day) by Russet Burbank potatoes during the 160-d growing season near Hermiston, Oregon. Daily nutrient accumulation rates of the Russet Burbank potatoes increased from 0 when planted to maxima (lb/A/day): K 14, N 6.5, Ca 4, P 0.9, dry matter 12.5, and then declined to 0 or nearly 0 at 160 days after planting (DAP). Translocation of N from the vines to the tubers of a crop of Russet Burbank potatoes grown near Becker, Minnesota is reflected in curves of figures showing an increasing daily rate of accumulation of N in the vines from 30 DAP to a maximum of about 4.5 lb N/A/day at 70 DAP, followed by a decline to about 0.5 lb N/A/day at 140 DAP. The daily rate of N accumulation in the tubers increased from 0 at about 42 DAP to a maximum rate of accumulation of slightly less than 6 lb N/A/day at 140 DAP.

In an experiment to investigate effects of moisture stress and N availability on relationships between the source (leaves) and sink (tubers) of photosynthate (carbon-containing compounds) in potato (*S. tuberosum* L.), Li et al. (2016) grew virus-free plants of potato in loessal soil contained in pots. Treatments included well-watered (90% soil water content), moderate water stress (70% soil water content), serious water stress (50% soil water content) and three N treatments, that is, deficient N (0 g N kg^{-1} added to soil), sufficient N (0.2 g N kg^{-1} added to soil), and excess N (0.4 g N kg^{-1} added to soil). Net photosynthetic rate (μmol CO_2 m^{-2} s^{-1}) decreased from 25 days after transplanting soil (DAT) to 70 DAP for all levels of N stress (deficient, sufficient, or excess) at each level of water stress (well-watered, moderate stress, or serious stress). Considering tuber yield in the context of decreasing net photosynthesis rate, Li et al. concluded that, under the conditions of their experiment, although both source and sink capacities were both decreased by water stress, there was not enough source supply for sink growth, resulting in tuber yield being more limited by source than sink.

Using the first derivative of regression equations that estimated the amount of N accumulating in amino acid fractions of maize (*Z. mays* L.) grain during the first 36 d of reproductive growth, Crawford and Rendig (1982) demonstrated that the *opaque-2* gene increased the rate of accumulation (mg N d^{-1}, in the grain per plant) of lysine (LYS) N but decreased the rates of accumulation of N in the methionine (MET), tyrosine (TYR), isoleucine (ILE), phenylalanine (PHE), serine (SER), proline (PRO), alanine (ALA), and leucine (LEU) fractions. Using the second derivative of the regression equations, they estimated that the maximum rate of N accumulation occurred earlier for the TYR, SER, PRO, ALA, LEU, and glutamate (GLU) fractions of the *opaque-2* grain, compared to the normal grain. From NH_4^+-N released during acid hydrolysis, it was estimated that the GLU and aspartate (ASP) residues in the grain of the two genotypes were amidated to the same extent until 20 DAP, but that thereafter, the percentage of amidated residues was greater in the grain of the normal counterpart.

16.4 MULTI-COMPARTMENT MODELS OF PLANTS

16.4.1 Compartments and Concepts of Influx, Efflux, and Net Flux In and Among Plants

The concept of intra-plant, inter-root competition includes overlapping nutrient depletion zones around roots, but it

does not include the spatial pattern of root exudates that can increase nutrient availability (De Parseval et al., 2017). Using the PARIS model of Raynaud et al. (2008), De Parseval and co-investigators simulated P uptake by a population of roots that can increase P availability by exuding citrate. They found that relationships between root uptake efficiency and root length density indicated root competition or facilitation, and their simulations showed a continuum between inter-root competition and facilitation. Two-dimensional figures depict patterns of P depletion territories, locations of roots, and gradients of citrate exuded by roots for three exudation rates (10^{-10}, 10^{-9} and 10^{-8} mmol cm^{-2} s^{-1}) and two root densities (5 or 50 cm cm^{-3}). Other figures depict P concentration [$C_p \times 10^5$ (mmol cm^{-3})], P supply [$S_p \times 10^{10}$ (mmol cm^{-3} s^{-1})], and citrate concentration [$C_c \times 10^4$ (mmol cm^{-3})] as a functions of distance to rhizoplane (mm) for one root and as functions of distance to left rhizoplane (mm) for two roots.

De Schepper and Steppe (2010) developed and tested a mathematical model with the main purpose to describe water transport through the xylem and sugar transport through the phloem in an entire living tree. The model is also able to simulate stem diameter variations, which result from both concurrent transport processes. Test species from which measurements were taken to test the model are a 3-year-old *Quercus robur* L. (oak) growing in a 50.0-L container in a growth chamber and an 89-year-old *Fagus sylvatica* L. (beech) tree growing in a mixed deciduous experimental forest. The authors provide a model schematic with model components (conductive xylem, conductive phloem, storage cells, and cambial zone) and water (full line) and sugar (dotted line) transport. Also included are a table of symbol, unit, and description of the model variables and another table of symbol, unit, and description of the model parameters. Various equations of the model are also presented.

To evaluate crop load effects on stem diameter variations and fruit growth in peach, De Swaef et al. (2014) developed a water (xylem) and carbon (phloem) transport model using existing models. Their model includes three vertical plant compartments *j* [stem (+roots), crown and fruit] and two radial compartments *i* [xylem (subscript X) and phloem (subscript P)]. For simplicity, no distinction was made between the stem and the roots, so they were merged into a compartment that was designated the stem compartment. The figure representing the compartments of the model includes the soil for which nonlimiting soil water availability conditions are assumed with soil water potential (Ψ_{soil}; [MPa]) being constant. Tables with symbol, unit, and description of model parameters and model variables are included as are equations defining relationships used in the model. A particularly useful table includes symbols, units, and estimated or literature value of the plant model parameters and makes references to sources of values from the literature. This modeling approach enabled De Swaef et al. to relate differences in crop load to differences in xylem and phloem water potential components at the stem and crown levels.

In order to develop a soil-plant model that does not oversimplify the representation of soil chemical processes or the root system, Gérard et al. (2017) coupled a root system architecture (RSA) model with a reactive transport model using a macroscopic approach. The two models were coupled using Fortran-C++ interoperability, and the resulting model was used to investigate P acquisition from hydroxyapatite in an alkaline soil as induced by P and Ca uptake and pH variations in the root zone. They present kinetic parameters used by the reactive transport model MIN3P that include parameters for (1) geochemical processes and (2) plant processes. For example, the Michaelis–Menten kinetic constant for the uptake of P and Ca is abbreviated $k_{M,P/Ca}$ with a value of 8.5×10^{-11} mol m^{-1} root s^{-1}.

In their investigation of the regulation of sulfate assimilation and metabolism in *Flaveria* spp (marigold), Gerlich et al. (2018) found, by interspecies grafting experiments, that the root system primarily controlled sulfate acquisition, glutathione (GSH) synthesis, and allocation of sulfate and metabolites in C_3 and C_4 plants. They found that sulfate reduction and GSH synthesis seed to be preferentially localized in the roots of C_4 species, which they opine may be linked to its colocalization with the phosphorylated pathway of serine biosynthesis. Twenty-day-old seedlings of five *Flaveria* species were resupplied for 4 h with 0.2 mM [^{35}S]-sulfate nutrient solution after 6 d exposure to low sulfate (20 μM sulfate [S20]) or adequate sulfate (750 μM sulfate [S750]). Rate of uptake of [^{35}S]-sulfate was within the range of about 110–200 pmol mg^{-1} FW h^{-1} for the four species of *Flaveria* treated with S20, and for the same four species treated with S750, uptake rates of [^{35}S]-sulfate were within the range of about 50–80 pmol mg^{-1} FW h^{-1}. Rates of uptake of [^{35}S]-sulfate were similar for *F. robusta* corresponding to the S20 and S750 pretreatments.

In a theoretical analysis of phloem transport based on the Münch hypothesis, Hölttä et al. (2009) developed a coupled xylem–phloem transport model. Their model includes the movement of solutes in xylem and phloem that help regulate the movement of sugars from photosynthesis via the phloem and movement of water containing minerals as a result of the water potential gradient driven by transpiration. Considerable attention is devoted by Hölttä et al. to the role of potassium that can move from xylem to phloem and from phloem to xylem as a solute with little viscosity that can help regulate osmotic potential

of the phloem to ensure movement of water from xylem to phloem for maintenance of turgidity and movement of more viscous solutes away from sources (sites of photosynthesis) to sinks elsewhere in the plant.

A mathematical model of water movement in the xylem was developed by Hong et al. (2017). The velocity of water movement within the plant stem is described, using some simplifying assumptions, but in as detailed a manner as possible using all major forces involved. The investigators propose a full mathematical model to calculate and predict the velocity of water movement through the xylem of plants. They tested the model with the experimental use of magnetic resonance imaging (MRI) and they claim that the predictions of the mathematical model and experimental results agreed "perfectly." The average velocity in the xylem was calculated to be 0.13 mm s^{-1}. Despite their claim, the authors declare that there are still some errors in the mathematical model, that is:

1. Some minor forces such as the root pressure are ignored, even though they may still, more or less, contribute to the water migration process.
2. The simplification of wall structures in friction calculation could cause some errors.
3. The plant used in their work was not tested for all the parameters used in the mathematical model.

Using $^{13}NO_3^-$ and $^{13}NH_4^+$ in short-term experiments because of the short half-life of ^{13}N, Kronzucker et al. (1999) measured fluxes of the two ions to describe cellular turnover kinetics, patterns of flux partitioning, and cytosolic pool sizes in seedling roots of rice (*O. sativa* L. cv IR72) supplied simultaneously with the two N sources. Plasma membrane fluxes of NH_4^+, cytosolic NH_4^+ accumulation and NH_4^+ metabolism were enhanced by the presence of NO_3^-, however, NO_3^- fluxes, accumulation, and metabolism were strongly repressed by NH_4^+. Both net N acquisition and N translocation to the shoot, however, were substantially greater when both ions were provided, compared to when NO_3^- or NH_4^+ was provided alone in identical concentrations. Compartmental analyses by efflux indicated three subcellular compartments identified by Kronzucker et al. as a surface film (I), a binding component in the cell wall (II), and the cytoplasm (III). In representative semilogarithmic plots for the three phases of efflux in the release of $^{13}NO_3^-$ [log (cpm released) g^{-1} h^{-1}] versus time of elution (0–22.5 min) for roots of intact cv IR72 rice seedlings maintained at 100 μM $[NO_3^-]_o$ with NH_4^+ or without NH_4^+, the efflux rates of $^{13}NO_3^-$ from the three subcellular components were measured within the range of 3.0–6.0 [log (cpm g^{-1} min^{-1})].

Nutrient loading of seeds is described by Murphy (2017), utilizing text and conceptual multi-compartment models. Figure 1 of Murphy's paper includes the anatomy of wheat (endospermic) and bean (non-endospermic) seeds and diagrammatic representation of a common cellular pathway of nutrient loading in seeds. Figure 2 is a diagrammatic representation of temporal aspects of cell division, cell expansion, and storage product accumulation after anthesis during the pre-storage and storage phases of nutrient loading in seeds. Figure 3 is a conceptual model of the pressure-flow hypothesis of phloem transport, showing key transport events in seed loading of nutrients. Figure 4 is a multi-compartment model showing membrane transport of nutrients between maternal and filial seed tissues occurring through channels or carriers. Figure 5 is a mechanistic model describing the integration of nutrient transport to and within developing legume seeds. Although quantitative data are absent from this paper, Murphy presents a robust and complex conceptual overview of various aspects of nutrient loading of seeds.

In 8- to 14-d-old maize (*Z. mays* L.) plants, NO_3^- flux of the intact plants was measured from the product of the transpiration rate and the concentration of NO_3^- in the xylem (Shaner and Boyer, 1976). When the seedlings were deprived of NO_3^-, NRA decreased, as did NO_3^- flux and the content of NO_3^- in the leaves. When NO_3^- was resupplied to the roots, the values of all three parameters increased. Among the measurements of the other parameters, transpiration rates were measured within the range of about 1 and 9 g DW^{-1} h^{-1}, and NRA and NO_3^- fluxes were presented by the investigators as the percent of the initial values when treatments were applied to ambient air and to rooting medium to vary NO_3^- flux. Shaner and Boyer concluded that NO_3^- flux to the leaves from the roots played a much larger regulatory role than leaf NO_3^- from the vacuoles in controlling the level of NRA in the intact plants.

Two pioneer trees, *Morus bombycis* and *Acer buergeranium*, were grouped into four treatment groups, that is, relative photosynthetic photon flux density (RPPFD) 100% or 10% × nitrogen-rich or nitrogen-poor conditions, and they were grown in an experimental garden for 60–100 d (Sugiura and Tateno, 2011). A model was developed by the investigators to predict optimal leaf-to-root (L/R) rations and leaf nitrogen content (N_{area}), and the model predicted that optimal L/R is higher and N_{area} is lower in low-light than in high-light environments, when compared with the same N availability. From predictions of the model and data from pot experiments, they conclude that the two pioneer tree species regulated L/R and N_{area} to maximize relative growth rate (RGR) in response to the availability of N and light. The maximum photosynthetic rate (μmol m^{-2} s^{-1}) increased within the range of leaf N content (N_{area}) from 0 to 3 g N m^{-2}. The net assimilation rate (NAR, g m^{-2} d^{-1}) was greater for plants treated with

100% RPPFD than for plants treated with 10% RPPFD within the range of N_{area} from 0 to 3 g N m^{-2}.

16.4.2 Flux Rates in Multi-Compartment Models of Plants

In maize, net rates of accumulation and loss of nitrogen in various parts of the maize shoot during reproductive growth have been estimated by first derivatives of regression equations based upon periodic sampling and chemical determination of N content of various compartments of the multi-compartment system. Maximum rates of accumulation of total N in the grain were estimated to be approximately 80 mg N day^{-1} $plant^{-1}$, based upon estimated rates of accumulation of exogenous N and endogenous N in the grain. N fluxes (net flux resulting from influx and efflux) for the stem, leaves below the ear, leaves above the ear, shank, cob, and husk were also estimated, based on the first derivatives of the regression equations (Crawford et al., 1982).

Net rates of accumulation and loss of nitrogen in the China 17 sorghum ([*S. bicolor* (L.) Moench] genotype, which is an efficient user of nitrogen, were estimated, per plant, to have varied among the following ranges: the lowest half of the stalk, 0 to –40 g N $week^{-1}$; the third highest of the four sections of the stalk, +0.04 to –0.04 g N $week^{-1}$; leaves of the third highest of the four sections of the stalk, +0.08 to –0.03 N g $week^{-1}$; the fourth highest of the four sections of the stalk, +0.16 to –0.07 g N $week^{-1}$; the leaves of the fourth highest of the four sections of the stalk, +0.11 to –0.04 g N $week^{-1}$; and the grain, 0 to 0.12 N g $week^{-1}$. Comparable data for the sorghum genotype, TX623, show fluxes differ during the same period of growth for a less efficient user of nitrogen (Crawford, et al., 2009).

Flux rates of N, P, K, Cu, Fe, Mn, and Zn varied in the roots and shoots of cucumber (*C. sativus* L.) plants, as affected by deficiency, sufficiency, or toxicity of Mn. During the period of 43–58 days after germination, Mn deficiency caused the roots to change from sink to source of N and K on days 56 and 53, respectively, and caused the shoot to change from sink to source of P and Fe on days 57 and 58 respectively. During the same period, Mn toxicity caused the roots to change from sink to source of N, K, and Cu on days 46, 51, and 46, respectively and caused the shoot to change from sink to source of Fe on day 55 (Crawford et al., 1990).

Fluxes of C, N, and P in above-ground and below-ground organs of *Zizania latifolia* (Manchurian wild rice) considered as a multi-compartment system indicate that the plant is heterotrophic with a decline in its rhizome reserves from January through April and autotrophic from the end of April through senescence of shoots from October to December. Dormancy occurred from January through March (Asaeda and Siong, 2008). Rates of above-ground budgets (AGB) and below-ground budgets (BGB) for C, N, and P are expressed by Asaeda and Siong on an areal basis, that is, a defined quadrat 50 cm × 25 cm, and below-ground biomass was sampled from undisturbed soil blocks 50 cm × 25 cm × 25cm deep. Several C budgets are presented for *Z. latifolia*, and net rates of uptake of N are in the range, approximately, of –0.20 g N m^{-2} d^{-1} to +0.85 g N m^{-2} d^{-1} while net rates of uptake of P are reported in the range, approximately, of –0.25 g P m^{-2} d^{-1} to +0.80 g P m^{-2} d^{-1} with values of the abscissa being in months.

In the context of a three-compartment model (shoot, nodules, and root), Jeschke et al. (1984) measured exchange rates of mineral cations K^+, Mg^{2+}, Ca^{2+}, and Na^+ in the xylem and phloem between root and shoot of nodulated white lupin (*Lupinus albus* L., cv. Ultra). Respiration losses of C by nodulated roots were assessed and concentrations of C, N, and cations in xylem and phloem were assayed by collecting root bleeding xylem sap and phloem sap of stem base during the day and night at several times during the study. There was a substantial return of K^+ and Mg^{2+} translocated from shoot to root via the phloem, providing the roots more K^+ or Mg^{2+} than was required for growth. Rates of return flow to roots and circulation within the plant were small for Ca^{2+} and Na^+. The authors present figures showing flow rates among compartments, recirculation from phloem to xylem, and accumulation during growth (μmol g FW^{-1} h^{-1}) of C, N, K^+, Na^+, Ca^{2+}, and Mg^{2+}.

Relationships between the rate of carbon assimilation (photosynthetic rate, P_n, μmol CO_2 m^{-2} s^{-1}) and specific amounts of pyruvate orthophosphate dikinase (PPDK, g protein m^{-2}), chlorophyll (μmol m^{-2}), phosphoenolpyruvate carboxylase (PEP_c, g protein m^{-2}), thylakoid N (g N m^{-2}), and ribulose-1,5-bisphosphate carboxylase (Rubisco, g protein m^{-2}) during remobilization of N during grain filling of maize were studied by Mu et al. (2018). They found that P_n decreased dramatically at 30 days after silking (DAS) and 20 DAS for high-N (HN) and low-N (LN) treatments, respectively. Total N began to be remobilized at 30 DAS and 10 DAS in the HN and LN treatments, respectively. Nitrogen remobilization efficiency of the three enzymes, Rubisco, PEB_c and PPDK was within the range of 60–74%, whereas remobilization of thylakoid-N was 22%.

Five deciduous woody species and six herbs typical of open sunny habitats such as secondary forest, abandoned cropland and roadsides were investigated to determine relationships among specific leaf area (SLA, m^2 kg^{-1}), relative growth rate (RGR, g g^{-1} d^{-1}), area-based leaf nitrogen concentration (LNC_a, g N m^{-2}), leaf nitrogen productivity (LNP, g g^{-1} N d^{-1})and specific nitrogen absorption rate of roots (SAR, g N g^{-1} d^{-1}). A very strong,

statistically significant ($r^2 = 0.91$, $P < 0.001$) relationship was found between RGR (0.10–0.25 g g^{-1} d^{-1}) and SAR (0.02 to 0.08 g N g^{-1} d^{-1}), as described by the equation, $y = 2.48x + 0.05$, where x = SAR and y = RGR. In studying these relationships among the above variables, Osone et al. (2008) present functions described by equations, including r^2 and P values of both their experimental data and corresponding data of Reich et al. (1998a, b), Poorter and Remkes (1990) and Poorter et al. (1990, 1991).

Shinano et al. (2006) found that upon removing a sink for N, the panicles, of rice (*O. sativa* L.), absorption of NO_3^- from the soil, or N uptake, was stopped. They concluded that the uptake of N by the roots appeared to be regulated by requirements of the sink, regardless of the carbohydrate status of the roots. Pointing out that high root activity is important to achieve high productivity, they indicate, however, that N absorption activity of the roots must relate to a high N demand of the shoot. When panicles were removed, root N concentration increased and was significantly higher in the panicle removal treatment than in the control. After panicle removal, retardation of leaf senescence was not observed, and N concentration in the leaves continued to decrease, irrespective of cytokinin level in the xylem. N uptake rate (ΔN, g N m^{-2} d^{-1}) and specific absorption rate of N in the roots (SARN, g N g RW^{-1} d^{-1}) decreased to a greater extent when panicles were removed, compared to the control with panicles intact.

16.5 RATES OF TRANSPORT OF ELEMENTS OTHER THAN ESSENTIAL PLANT NUTRIENTS

Shaibur et al. (2012) investigated effects of arsenic (As) at concentrations of 0, 6.7, 33.5, and 67 μM As on concentrations (nmol mL^{-1}) in the xylem fluid and rates of translocation (pmol $plant^{-1}$ h^{-1}) of nine mineral nutrients (P, K, Ca, Mg, Cl, Fe, Mn, Zn, Cu) and As in barley seedlings. The flow rate of xylem fluid decreased significantly ($P < 0.05$) from about 70 μL $plant^{-1}$ h^{-1} of the control to about 5 μL $plant^{-1}$ h^{-1} at the highest level of As (67 mM) in the nutrient solution. The authors speculate that reduction in the flow rate of the xylem fluid was probably due to reduction of the shoot and root growth caused by As toxicity and the harmful effect of As on the loading site of the xylem sap. The most rapid translocation of As, 27.0 pmol $plant^{-1}$ h^{-1}, occurred with the 6.7 μM As treatment, and the As translocation rates with the 33.5 and 67 μM As treatments were 12.3 and 17.2 pmol $plant^{-1}$ h^{-1}; all three xylem translocation rates of As were significantly different ($P = 0.05$) from one another.

Toxic levels of Cd, a pollutant in rice (*O. sativa* L.) production areas of China, were reported in 44% of rice samples from Guangdong Province in 2014. In some locations, Cd levels in the soil were found to be >200 times the national health standard (Tatlow, 2014). Japanese researchers Fujimaki et al. (2010), using non-invasive imaging, characterized absorption, transport, and accumulation of Cd in intact rice plants. The rates of absorption of Cd were found to be proportional to Cd concentrations in the culture solution within the range of 0.05 to 100 nM, and Cd moved through the xylem in the shoot organs with velocities of a few cm h^{-1}, rates slower than the bulk flow of the xylem. Fujimaki et al. (2010) described the rate of absorption by the roots (pmol h^{-1}) as a function of the amount of Cd absorbable Cd in the culture solution (pmol) at time t(h): $v(t) = -\mathrm{d}a(t)/\mathrm{d}t$ and they assumed that the Cd absorption they measured was probably mediated by transporters and could be described by Michaelis–Menten kinetics. On that basis, they developed equations describing proportionality between absorption rate and concentration of Cd, $v(t) = k[a(t)/V]$, where k and V denote the coefficient of proportionality (ml h^{-1}) and the culture volume (ml), respectively. Additional equations are derived by the investigators.

In another investigation of Cd in rice (*O. sativa* L.), Wu et al. (2018) concluded that increasing NH_4^+ nutrition contributes to the inhibition of Cd uptake, xylem transport, and subsequent accumulation. They investigated physiological and genetic mechanisms of Cd uptake by roots, xylem translocation, and subsequent Cd accumulation in rice affected by different NO_3^-/NH_4^+ ratios under low and high Cd stress. Total Cd accumulation in the whole plant decreased with the high NH_4^+-N rations (NO_3^-/NH_4^+, 1:2 and 0:1). The rate of net Cd^{2+} influx at the root hair zone from 240 to 360 s was within the range of –0.2 to –0.6 pmol cm^{-2} s^{-1} for all treatments when the rice seedlings received pretreatment with NO_3^-/NH_4^+ (1:1) followed by treatment with NO_3^-/NH_4^+ at any of the following ratios: 1:0, 2:1, 1:1, 1:2, or 0:1; the highest rate, that varied from about –0.5 to –0.6 pmol cm^{-2} s^{-1}, occurred with the 1:0 treatment, and the lowest rate, that varied between about –2.5 to –3.5 pmol cm^{-2} s^{-1}, occurred with the 0.1 treatment.

In the United States and Canada, high Cd content in durum wheat (*T. turgidum* L. var durum) is a source of potential health and economic problems for consumers and growers. Comparing *T. turgidum* var *durum* with *T. aestivum* L. (bread wheat) (Hart et al., 1998). During a 24 h period with roots immersed in a solution that included 170 nM Cd, after 4 h, at any point in time, translocation of Cd was greater to the shoot of *T. aestivum*, compared to *T. turgidum* var *durum*. With an increasing Cd^{2+} activity from 0 to 1300 nM, Cd^{2+} uptake of both cultivars of wheat, linear and saturable components of Cd^{2+} uptake were plotted, and V_{max} and K_m values of saturable components

were calculated by fitting a hyperbolic curve function to the saturable points. V_{max} for bread wheat was 26 ± 2 nmol g^{-1} h^{-1} and for durum wheat was 29 ± 2 nmol g^{-1} h^{-1}.

Sedum alfredii Hance (Crasulaceae) is the only known Cd-hyperaccumulating species that is not in the Brassica family. Lu et al. (2008) used radioactive techniques, metabolic inhibitors, and fluorescence imaging to contrast Cd uptake and translocation between a hyperaccumulating ecotype (HE) and a non-hyperaccumulating ecotype (NHE) of *S. alfredii*. The K_m of ^{109}Cd influx into the roots was similar for HE and NHE, but the V_{max} (approximately 4 μmol g root DW^{-1} h^{-1}) in the HE at 50 μmol Cd L^{-1} external concentration was twofold higher than in the NHE. The rate of translocation of ^{109}Cd from the root to shoot in the HE was >10 times higher than that of the NHE, and the shoots of the HE accumulated ^{109}Cd concentrations much higher than those of the NHE.

Cesium ion (Cs^+) competes with K+ for uptake by plants (Genies et al. 2017). Observing uptake of Cs^+, as affected by the presence of K^+ in the nutrient solution, by two genotypes of *A. thaliana*, Genies et al. measured Cs^+ uptake rate during pre-culture and during exposure of the plants to Cs^+, that is, 10 μM K^+ or 3000 μM K^+. Rates of Cs^+ uptake were measured within the range of 1 to 10,000 nmol Cs^+ g^{-1} FW roots h^{-1} as a function of external Cs^+ concentrations within the range of 0.1–1000 μM Cs^+.

Selenate and selenite are absorbed differently in the roots of wheat. Plants absorbed similar amounts of selenium (Se) within 1 d when supplied with selenite or selenate. Uptake of selenate and selenite was enhanced in sulfur-starved and phosphorus-starved plants, respectively. During a 30-min period when selenite concentration was increased from 0 to 10 μM, Se uptake rate increased from 0 to about 7 mmol Se g^{-1} root h^{-1} when no phosphorus was present, but when 0.1 mM phosphorus was present, Se uptake rate increase from 0 to only about 2 mmol Se g^{-1} root h^{-1}; the investigators surmised that selenite is absorbed by a mechanism similar if not identical to that of phosphate (Li et al., 2008).

Sodium transport in *T. turgidum* L. subsp. *durum* (durum wheat) was studied by Davenport et al. (2005) who considered the plant at the three-leaf stage to be a multi-compartment system composed of root and shoot composed of leaf sheaths, the shoot apex, and leaf meristems. The leaves are described as being divided into sheath and blade by the ligule. Rates of Na^+ fluxes were measured for the following: plasma membrane influx (nmol g FW^{-1} min^{-1}), tonoplast influx (nmol g FW^{-1} min^{-1}), shoot uptake (nmol g root FW^{-1} min^{-1}), root efflux (nmol g FW^{-1} min^{-1}) for plasma membrane and tonoplast, and relative efflux (min^{-1}) for plasma membrane efflux (min^{-1}) and tonoplast efflux (min^{-1}). Salt-tolerant landrace 149 and salt-sensitive cultivar Tamaroi were compared, and the rate of transfer of $^{22}Na^+$ from root to shoot, or xylem loading, was much lower in salt-tolerant landrace 149, and the leaf sheath of the salt-tolerant genotype had a greater capacity to extract and sequester Na^+. The two genotypes did not differ significantly in unidirectional uptake of Na^+ by the roots and apparently did not recirculate Na^+ from shoot to roots. The authors suggest that xylem loading and leaf sheath sequestration are separate genetic traits that may interact to control leaf blade Na^+. Sodium flux rates in the roots have been measured at rates greater than 250 nmol m^{-2} s^{-1} (Yeo and Flowers, 1986).

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