17 Rates of Processes of Essential Plant Nutrients

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CONTENTS

17.1 INTRODUCTION

The goal of the present chapter is to give the reader a clearer sense of some of the many processes that involve mineral nutrients and ranges of rates at which those processes occur. Mineral nutrition of plants involves the acquisition of elements from the environment, and the organization and functioning of essential plant nutrients are a consequence of the interaction of deoxyribonucleic acid (DNA) of the plant with the environment. Because of the great complexity of plants, processes involving essential nutrient elements vary from relatively slow to relatively fast. Plants require 17 essential nutrients, and several other elements, such as cobalt, sodium, and silicon, have been found to stimulate the growth of some plants (Epstein and Bloom, 2005).

Green plants obtain carbon from the air, whereas nonphotosynthetic plants such as fungi obtain carbon as saprophytes, breaking down organic materials of living or dead organisms. Unicellular and multicellular, photosynthetic, nonvascular plants such as algae obtain carbon and other essential elements with little transport from the environment to the site of photosynthesis, and 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 distance far greater than the dimensions of the uncharged atoms, molecules, or ions containing the essential plant nutrients. The anatomy of vascular plants as well as nonvascular plants can be understood to include sources and sinks, between which mineral nutrients move. In addition, the plant itself 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.

Several means of measuring rates of transport of mineral nutrients in plants, other than velocity, include volume transfer ($cm^3\ h^{-1}$), mass transfer ($g\ h^{-1}$), and specific mass transfer ($g\ cm^{-2}\ h^{-1}$) (Canny, 1960).

17.2 MOVEMENT OF ELEMENTS INTO WHOLE PLANTS AND COMPARTMENTS OF MULTICOMPARTMENT PLANTS

Within a range of concentrations from 0.1 to 10,000 mmol m^{-3}, net rates of uptake of Ca^{2+}, K^+, N, P, S, and Zn^{2+} were found to range from less than 0.001 to greater than 1.0 μmol g FW $root^{-1}$ h^{-1} (Pitman, 1975). In maize, net rates of accumulation and loss of nitrogen in various parts of the maize shoot during reproductive growth have been estimated by the first derivatives of regression equations based upon periodic sampling and chemical determination of N content of various compartments of the multicompartment system. Estimated 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 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 (*Sorghum bicolor* (L.) Moench) genotype, which is an efficient user of nitrogen, were estimated, per plant, to have varied among the following ranges: lowest half of the stalk, 0 to −40 g N $week^{-1}$; 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 g N $week^{-1}$; fourth highest of the four sections of the stalk, +0.16 to −0.07 g N $week^{-1}$, leaves of the fourth highest of the four sections of the stalk, +0.11 to −0.04 g N $week^{-1}$; and the grain, 0–0.12 N g $week^{-1}$. Comparable data for the sorghum genotype, TX623, show that 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 (*Cucumis 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).

Mycorrhizal associations with plant roots have been shown to increase the uptake of phosphate. 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 nonmycorrhizal 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 nonmycorrhizal uptake, which was 0.042 pmol cm^{-1} s^{-1}.

Eight-day-old maize (*Zea mays* L.) seedlings replete with nitrogen, when placed in N-deficient solutions, increased their rate of absorption of nitrate and ammonium 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 ammonium increased from about 5 to 9 μmol g^{-1} h^{-1}, whereas the rate of uptake of nitrate 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).

Selenate and selenite are absorbed differently in the roots of wheat. Plants absorbed similar amounts of 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 increases 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). Selenate and sulfate are oxyanions of selenium and sulfate, respectively, and are in Group 6A of the periodic table. These two elements both have oxidation states of +4, +6, and −2 and display similar chemical behavior.

17.3 MOVEMENT OF ESSENTIAL NUTRIENT ELEMENTS IN PLANTS

Three categories of movement of essential elements in vascular plants are (1) movement across membranes of cells and or organelles such as the plasmalemma, mitochondrion, and vacuoles; (2) longer-distance transport through the vascular system composed of xylem and phloem; and (3) movement through stomata and cuticle of leaves.

17.3.1 Rates of Transport of Essential Plant Nutrients across Cell Membranes

Rates and patterns of ion absorption by plant roots from the soil solution are partially influenced by 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 sugarcane (*Saccharum officinarum*) and found that as the concentration of phosphate outside the plant increased, it finally reached a maximum rate of absorption. Subsequently, Emanual Epstein and C. E. Hagen described the transport of ions across cellular membranes in terms used in enzymology (Epstein and Hagen, 1952). 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 counterflow 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 others 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, $v = \frac{1}{2}V_{max}$. So, $V_{max}/2) = (V_{max} \cdot [S])/(K_m + [S])$, $(K_m + [S]) = 2[S]$, and $K_m = [S]$. So, 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 and others demonstrated that during the absorption of potassium, when increasing the concentration of K^+ in the substrate from 0 to 50 mM, by barley roots, 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 and others 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 0–40 μmol g^{-1} h^{-1}. Welch and Epstein (1968, 1969) concluded that both mechanism 1 and mechanism 2 exist in parallel across the plasmalemma. A recent 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 potassium can be absorbed via a number of different kinds of channels in cell membranes. Following the pioneering work of Epstein and others, subsequent research has linked such factors as root:shoot ratio and relative growth rate to nutrient uptake rate (v), maximum uptake rate (v_{max}), and uptake rate of the whole plant (v_{plant}) (Gutshick and Pushnik, 2005). For zinc, 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 zinc across membranes is collected from many investigators using various crop species under various conditions to measure zinc flux.

Effects of external concentration of nutrient ions upon 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, the concentration of the ion in the compartment is maintained at an adequate level, and the uptake rate declines to a steady rate (Glass and Siddiqi, 1984). Other changes in the uptake rates of nutrient ions are diurnal, such as the case of net nitrate 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).

The pH of the soil solution has been shown to affect the rate of absorption of potassium. In studying the effect of pH on the 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 mineral nutrients from the environments influenced by key factors such as pH of the solution in contact with the organs of the plant that absorb the nutrients directly from the environment.

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 (f FW roots)$^{-1}$ day^{-1} with no K^+ present to about 100 ng atoms (g FW roots)$^{-1}$ day^{-1} when 750 μM K^+ was present with the concentration of Ca^{++} less than 1000 μM. The rate of K^+ absorption was approximately the same, about 30 ng atoms (g FW roots)$^{-1}$ day^{-1} when Ca^{++} was present, regardless of whether K^+ was present or not in the solution from which the zinc was absorbed.

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 the uptake of ions by the roots. The rate of absorption of potassium by the roots of sunflower, *Helianthus 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 potassium returned to greater than 0.140 mequiv h^{-1} once the temperature of the phloem was returned to its original temperature (Weatherly, 1969). Weatherley et al. 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. It is possible, however, that the cooler phloem reaching the roots may have depressed the rate of K^+ absorption due to the lower temperature within the roots, since the rate of absorption of mineral nutrients has been shown to be temperature-dependent (Sutcliffe, 1962). The external concentration of KCl ranging from 0 to 80 mM resulted in rates of influx of Cl^-, which increased from 0 to approximately 10×10^{-13} mol cm^{-2} s^{-1} across the plasmalemma and from 0 to approximately 1.4×10^{-13} mol cm^{-2} s^{-1} into the vacuole of cells of maize. A similar pattern was evident for the influx of Cl^- across the plasmalemma and into the vacuole of carrot cells (Cram, 1974).

The rate of uptake of mineral 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° rise in the temperature. Absorption of mineral 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°C–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 fairly 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 to 4 μequiv (g fresh wt.)$^{-1}$ from 2 to 6 h later at 2°C, the rate of uptake having gone to essentially 0 at 2 h. On the other hand, the amount of K^+ absorbed continually increased from 0 to 16 μequiv (g fresh wt.)$^{-1}$ 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.)$^{-1}$ to a maximum of about 7 μequiv (g fresh wt.)$^{-1}$ at 40°C, but was about 5 μequiv (g fresh wt.)$^{-1}$ 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.)$^{-1}$ at 2°C but increased to about 12 μequiv (g fresh wt.)$^{-1}$ at 40°C, but the amount of K^+ absorbed was only about 3 μequiv (g fresh wt.)$^{-1}$ at 50°C (Sutcliffe, 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 mineral nutrients across cell membranes.

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 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 the uptake of mineral nutrients by photosynthetic plants and illustrates the diurnal fluctuation of 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.

Uptake of inorganic phosphate, P_i, is affected by external P_i concentration. *Spirodela* 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 the same species of the control treatment when 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 Pi 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}. Temperature has also been shown to affect the uptake of P_i by *Spirodela*. When the alga was exposed to 1000 μM Pi, 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).

Aerobic organisms such as green plants require oxygen to absorb ions (Mengel and Kirkby, 1978). It was shown that the rate of absorption of phosphate increased from 0 to about 3 mol $P \times 10^{-7}$ (g root)$^{-1}$ h^{-1} as the oxygen tension was increased from 0% to about 2.4% (Hopkins, 1950). This is but one example of the necessity of oxygen for active uptake of a mineral nutrient across cell membranes.

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 mineral nutrients increased significantly: 3.3-fold for NO_3^-, 2.2-fold for Ca^{2+}, 4-fold for K^+, and 2.5-fold for inorganic P. According to Glass (2005), following the 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 "upregulate" and "downregulate" uptake rates of mineral nutrients, plants may be able to minimize fluctuations of availability of mineral nutrients within the plant. Since concentrations of mineral 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.

The mechanism for nitrate ion uptake into barley (*Hordeum vulgare*) plants was investigated, and the net uptake rate of nitrate by barley plants that had previously received little nitrogen decreased from approximately 2 μmol NO_3^- g^{-1} min^{-1} to slightly more than 0 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 nitrate 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 by Shingles et al. (2004) to be about 3.3 μL (mg chlorophyll)$^{-1}$ (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^+, 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.

17.3.2 Rates of Transport of Essential Plant Nutrients in 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}). The xylem of vascular plants is the specialized tissue that conducts solutes from the root to shoot; it not only can be considered a continuous system of interconnected tubes with little resistance to the flow of water but also includes living parenchyma cells that 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 Pi movement in xylem vessels is about 200 cm h^{-1}, and phosphorus redistribution in vascular plants is very rapid, the transport of Pi in the phloem occurring at a rate of about 50 cm h^{-1} (Kolek and Kozinka, 1992), and in maize plant xylem, 79%–82% of the total activity of ^{32}P-compounds transported in xylem exudate was inorganic phosphorus, 3%–7% was the fraction of phosphoric esters of glycides, and 13%–17% was free nucleotides (Michalík and Ivanko, 1971). Sodium flux rates in the roots have been measured at rates greater than 250 nmol m^{-2} s^{-1} (Yeo and Flowers, 1986).

Root pressure exudation experiments 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 (Anderson, 1975). Values of J_s reported by different investigators for K^+, Cl^-, SO_4^{2-}, NO_3^- in xylem exudates of *Zea mays*, *Ricinus communis*, *Sinapis alba*, *Triticum aestivum*, *Avena fatua*, *A. sativa*, *H. annuus*, and *Allium cepa* are organized in tabular format by Anderson (1975).

Sieve tubes of the phloem carry both organic compounds synthesized in the leaves and inorganic ions. Zimmerman 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} (Zimmermann, 1969). 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 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 dry weight cm^{-2} phloem h^{-1}.

In the phloem, different 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 $^{14}CO_2$, titrated 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 mineral requirements of the plant by maintaining osmotic potential of 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 shoot cells, and they resemble indole-3-acetic acid (IAA) in their physiological action (Marumo, 1986). Auxin moves 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 that they measured range from ~5 to 50 μg C d m^{-2} min^{-1} for a range of net photosynthesis rate from 0 to ~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*.

17.3.3 Acquisition of Elements through Stomata and Cuticle of Leaves

Carbon dioxide moves into leaves through stomata, and the uptake of CO_2 is regulated, in large part, by diffusion (Gastra, 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 0 (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 1 s; 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 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 estimate that CO_2 would move through stomata at a rate of 60 mg CO_2 dm^{-2} h^{-1}. Wiitjacsono et al. (1999) measured the assimilation of CO_2 by *in vitro* and *ex vitro* 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}), 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).

Organic liquids (Stalfelt, 1916), and particularly oils (Turrell, 1947) with low surface tension, undoubtedly infiltrate stomata. Aqueous solutions with a surface tension near that of pure water (~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 (1961) 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 the stomatal route. *Phaseolus vulgaris* L. leaves, 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 C^{14}-labeled urea during a 5-min period were 234 counts min^{-1} (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 and 155 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 absorption of $^{59}Fe^{3+}$ 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 iron per unit dry weight or per unit of leaf area. There were distinct differences in rates of uptake of iron by the four different plant species. Use of a surfactant caused a large increase in iron uptake in both the sorghum and the red kidney bean leaves during the day. An increase also occurred due to 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 substomatal 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 substomatal 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 $^{45}Ca^{2+}$, $^{86}Rb^{+}$ (an analogue for K+), $^{36}Cl^{-}$, and $^{35}SO_4^{2-}$ 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 monovalent cations was investigated using isolated leave cuticles of apricot (*P. armeniaca* L.). The penetration rates of the monovalent cations in group IA followed a normal lyotropic series, that is, $Cs^+ > Rb^+ > K^+ > Na^+ > Li^+$. 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 × hour 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).

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