TRANSPORT OF WATER AND NUTRIENTS IN PLANTS

W.E. Riedell

Plant Physiologist, U.S. Department of Agriculture, Agricultural Research Service, Brookings, South Dakota, USA

T.E. Schumacher

Professor, Plant Science Department, South Dakota State University, Brookings, South Dakota, USA

Keywords: Xylem, phloem, vascular system, sieve element, companion cell, carrier molecules.

Contents

- 1. Introduction
- 2. Source-Sink Relationships
- 3. Phloem Loading and Unloading
- 4. Driving Gradients and Transport Processes
- 5. Carrier Molecules and Sequestration

Glossary

Bibliography

Biographical Sketches

Summary

In plants, the organs that absorb water and inorganic nutrients from the soil (roots) are separated from those that capture energy from the sun (leaves). In order to thrive in a terrestrial habitat, plants must coordinate the physiological processes that occur in the roots with those that occur in the leaves. Uptake of water and soil inorganic nutrients by roots is interdependent with the leaf assimilation activities (release of water, gathering of carbon dioxide and solar energy, and photosynthesis). The transport of materials throughout the plant body provides the physiological basis for this coordinated interdependence. This article contains five sections related to the transport of water and nutrients in plants: Introduction, Source-Sink Relationships, Phloem Loading and Unloading, Driving Gradients and Transport Processes, and Carrier Molecules and Sequestration.

A general description of transport processes in plants is presented in the Introduction. This general description outlines the physiological and structural components of plant transport processes. The section on Source-Sink Relationships discusses the mass-flow hypothesis and the extrapolation of this hypothesis to living plants. Anatomical, physiological, and biochemical characteristics of phloem transport are presented in section 3. The physiological basis of transport and the physical processes of convection and diffusion are discussed in section 4. The biochemistry and physiology of the main types of transporters are discussed in section 5. This section discusses ATPases, channel proteins, carrier proteins, uniporters, antiporters, and symporters.

1. Introduction

As a generalization, mineral nutrients and water are taken up from the soil and transported upward, whereas products of photosynthesis (photosynthate) are produced in green leaves and transported downward. Mineral nutrients and water move in the plant through a series of tissues, beginning at the root hairs, which absorb water from the soil, through the trachieds and vessel elements of the vascular system (collectively called the xylem), and ending in the parenchyma cells which release water to the leaf intercellular spaces.

Tracheids are elongated, non-living cells (at maturity) that have thickened secondary cell walls. Their end walls are tapered but not perforated while their side walls contain many pits. When functional, trachied pits are aligned so that water and solutes flow from tracheid to tracheid. Tracheids also have great tensile strength, and thus play an important role in providing structural support as well as in transport processes. Tracheids are the basic water and solute transport cells in gymnosperms.

Xylem vessel elements are highly modified solute and water transport cells. They are anatomically similar to tracheids, but they also have perforated end walls and pits of greater complexity. Thus vessel elements, when lined up end to end, can form elongated vessels up to several meters long (Figure 1). Vessel elements occur in most angiosperms but not in gymnosperms.

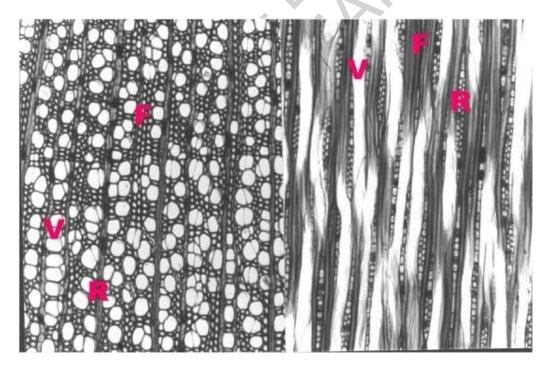


Figure 1. Light micrograph of American sweet gum tree wood showing vessels, fibers and ray cells.

The xylem fluid contains between 1 to 20 mg dry matter per ml, has an acidic pH (range of 5.2 to 6.5), and contains nitrogenous compounds synthesized in the roots as well as mineral nutrients. Xylem fluid also contains sugars, organic acids, and plant hormones.

For the most part, the transport of substances dissolved in the xylem fluid (solutes) is a passive process; the solutes are carried from roots to shoots with the transpiration stream. Thus, the velocity of xylem transport is governed by the rate of transpiration.

Photosynthate produced by leaves is transported downwards in a complex tissue called phloem. Phloem is composed of four cell types: parenchyma cells, fibers, sieve elements, and companion cells that are associated with sieve elements. Sieve elements, the basic transport cells of the phloem, are elongated cells similar to tracheids but are living at maturity (Figure 2). Sieve elements do not have a nucleus or a vacuole while their end walls and frequently their lateral walls have perforated regions called sieve areas. More highly evolved sieve elements have complex sieve regions called sieve plates (Figure 3). Sieve elements lined up end-to-end are called sieve tubes. Sieve elements are always associated with at least one living companion cell. There are many cellular connection tubes (plasmodesmata) between sieve elements and companion cells.

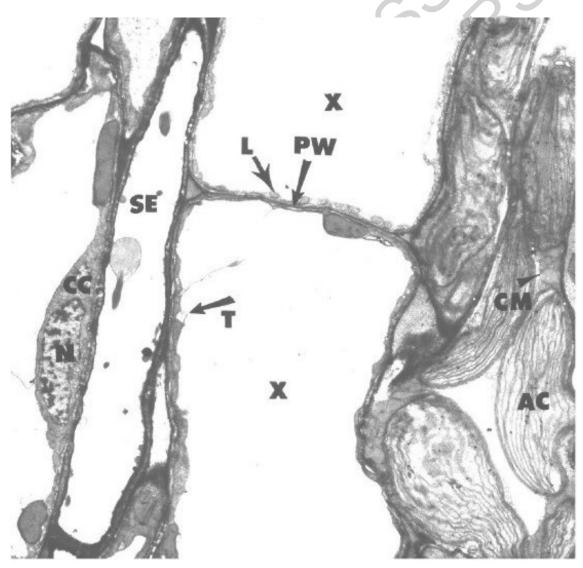


Figure 2. Electron micrograph of young maize leaf showing vascular elements and chloroplasts.

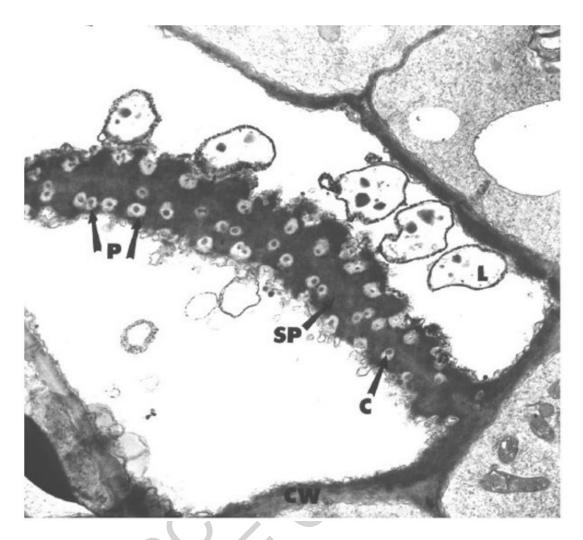


Figure 3. Electron micrograph of onion root tip showing phloem sieve element and sieve plate.

Fluid contained in the phloem has a solute concentration of 50 to 300 mg dry matter per ml and has an alkaline pH (8.0 to 8.4). About 80 to 90% of the total dry matter in phloem fluid is sugar. Nitrogenous compounds, amino acids, organic acids, inorganic nutrients, and plant hormones are also transported by the phloem. The velocity of phloem transport is about 5 times slower than that of xylem transport.

From both a physiological and a structural point of view, transport activities in the plant may be divided into two parts.

1) Transport of water and nutrients through cells. Examples of this include the movement of water from the soil solution through root cells to the vascular system and the movement of water from the vascular system through leaf cells to the intercellular spaces. Water moves for only short distances through cells. Short-distance transport, which is important in cell to cell interactions, probably takes place mostly by diffusion through plasmodesmata. In some cases, short-distance transport is an active process requiring energy expenditure by the cells. An example of active short-distance transport is phloem loading and unloading during sugar transport (see sections 3 and 4). The

living portions of plant cells (components within the cellular membrane e.g. cytoplasm and the sieve element conducting cells of the phloem) are considered to represent the symplasm.

2) Transport between roots and leaves. Long-distance movement of water and nutrients is mainly through the xylem tracheids and vessels and the phloem sieve elements of the vascular system (Figure 4). The xylem tracheids and vessels, which are dead cells, can be envisioned as a series of water-filled tubes. In herbaceous plants the distance of water movement through the xylem may be only centimeters while in trees the water may move through this system over 110 meters. The aqueous phase that lies outside of the cellular membrane (e.g. cell walls and the conducting cells of the xylem) are considered to represent the apoplast.

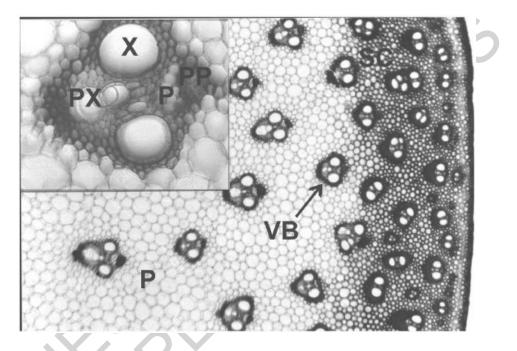


Figure 4. Light micrograph of maize stem showing vascular bundles, sclerenchyma cells, and parenchyma cells.

Transport processes in plants include water and inorganic nutrient uptake, the shortdistance transport of inorganic and organic nutrients from cell to cell, and the longdistance transport of water and nutrients throughout the plant by the vascular system. Water and inorganic nutrient uptake are covered in sections 2 and 3.

-

- -
- -

TO ACCESS ALL THE **16 PAGES** OF THIS CHAPTER, Visit: <u>http://www.eolss.net/Eolss-sampleAllChapter.aspx</u>

Bibliography

Arredondo-Peter R., Hargrove M.S., Moran J.F., Sarath G., and Klucas R.V. (1998). Plant Hemoglobins. *Plant Physiology* 118,1121-1125 [This manuscript provides an update on the biochemistry of plant hemoglobins]

Assmann S.M. (2001). From Proton Pump to Proteome. Twenty-Five Years of Research on Ion Transport in Higher Plants. *Plant Physiology* 125,139-141 [This short review of ion transport history is a delightful summary of the rapid progress that has occurred over the last 25 years of research with a view toward future research]

Chrispeels M.J., Crawford N.M., and Schroeder J.I. (1999). Proteins for Transport of Water and Mineral Nutrients across the Membranes of Plant Cells. *Plant Cell* 11, 661-676 [A very well written discussion of transport proteins with an excellent review of aquaporins, their role and physiology in plants.]

Cobbett C.S. (2000). Phytochelatins and Their Roles in Heavy Metal Detoxification. *Plant Physiology* 123,825-832. [An excellent review of the current state of knowledge about plant response to heavy metal stress]

Cohen C.K., Fox T.C., Garvin D.F., and Kochian L.V. (1998). The Role of Iron-Deficiency Stress Responses in Stimulating Heavy-Metal Transport in Plants. *Plant Physiology* 116,1063-1072. [This paper gives an overview of the two strategies used by plants to acquire iron from soils. Provides evidence that iron deficiency can stimulate the uptake of heavy metal ions by inducing an iron transport protein that may also facilitate uptake of other metals.]

Guerinot M.L. and Salt D.E. (2001). Fortified Foods and Phytoremediation. Two Sides of the Same Coin. *Plant Physiology* 125,164-167. [A stimulating discussion of the possible applications that may result from our increased understanding of transport proteins and newly developed genetic engineering techniques.]

Lalonde S., Boles E., Hellmann H., Barker L., Patrick J.W., Frommer W.B., and Ward J.M. (1999). The dual function of sugar carriers: transport and sugar sensing. *Plant Cell* 11,707-726 [A comprehensive examination of sucrose carrier proteins, their regulation, and role as sensors. Also an excellent overall review of plant sucrose apoplastic and symplastic transport systems.]

Maeshima M. (2001). Tonoplast Transporters: Organization and Function. 52,469-497. [An overview of the current state of knowledge concerning carrier proteins and molecular pumps in the tonoplast.]

Oparka K.J. and Turgeon R. (2000). Sieve Elements and Companion Cells – Traffic Control Centers of the Phloem. *Plant Cell* 11:739-750. [An excellent discussion of sieve elements and companion cells and the roles that the SE-CC complex plays in trafficking endogenous and foreign macromolecules. Includes detailed micrographs and figures.]

Oparka K.J. and Cruz S.S. (2000). The Great Escape: Phloem Transport and Unloading of Macromolecules *Annual Reviews of Plant Physiology and Plant Molecular Biology* 51,23-347. [Detailed information on the role and physiology of sieve tubes and companion cells in the phloem pathway. Provides up-to-date information on what is known and not known about macromolecule loading and unloading in the phloem tissues.]

Palmgren M.G. (2001). Plant Plasma Membrane H+-ATPases:Powerhouses for Nutrient Uptake *Annual Reviews of Plant Physiology and Plant Molecular Biology* 52,817-845. [An interesting review of the role of H⁺-ATPases in nutrient uptake. This paper contains some excellent diagrams and illustrations.]

Passioura J.B. (1988). Water Transport In and To Roots *Annual Reviews of Plant Physiology and Plant Molecular Biology* 39,245-265. [An excellent review that provides an interesting summary of radial and axial water transport across whole root systems.]

Turgeon R. (1989). The Sink-Source Transition in Leaves *Annual Reviews of Plant Physiology and Plant Molecular Biology* 40,119-138. [A detailed structural and mechanistic summary of the sink to source transition in developing leaves.]

Van Bel A.J.E. (1993). Strategies of Phloem Loading Annual Reviews of Plant Physiology and Plant Molecular Biology 44,253-281. [A comprehensive summary of phloem loading, including definitions, ultrastructural descriptions, and physiological mechanisms.]

von Wirén N., Klair S., Bansal S., Briat J.F., Khodr H., Shioiri T., Leigh R. A., and Hider R. C. (1999).

Nicotianamine Chelates Both Fe III and Fe II. Implications for Metal Transport in Plants. *Plant Physiology* 119,1107-1114. [A focused account of the role of nicotianamine in plant iron metabolism including a possible role as an iron scavanger]

Williams L.E., Miller A.J. (2001). Transporters Responsible for the Uptake and Partitioning of Nitrogenous Solutes. *Annual Reviews of Plant Physiology and Plant Molecular Biology* 52:659-688. [A comprehensive review of current knowledge about transport proteins involved with nitrate, ammonium, and amino acid transport.]

Biographical Sketches

W.E. Riedell is a Plant Physiologist with the U.S. Department of Agriculture, Agricultural Research Service in Brookings, South Dakota. Dr. Riedell has research experience in plant cell biology, ultrastructure, mineral nutrient relationships, and plant/insect interactions. Dr. Riedell's research activities are focused on two major areas. First, to investigate the effects of biotic and abiotic stresses on crop plant physiology and to develop integrated crop management systems that help reduce yield losses under stress conditions. Second, to develop a comprehensive understanding of crop response to rotation, tillage/residue management practices, and cover crops and to develop sustainable crop production systems.

T.E. Schumacher is a Professor of Soil Biophysics at South Dakota State University. Dr. Schumacher has research experience in soil biophysics, soil management, and plant physiology. Research activities are broken down into three areas: 1. The application of soil physics and plant physiology to agro-ecological problems; 2. The development of management practices that protect soil and water resources; and 3. Working with plant breeders to develop crops adapted to abiotic stresses. Of special interest is the interaction of plant root systems with the soil environment. These include studies of changes in root systems in response to physical alterations within the root environment. A second related area of interest is the change in soil physical environments caused by root systems. He is actively involved in the application of research results to soil and water conservation efforts.