# Measurement of Root Hydraulic Conductance

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Plant root systems provide water, nutrients, and growth regulators to the shoot. Growth and production of a plant are often limited by the ability of the root to extract water and nutrients from the soil and transport them to the shoot. The transport of most nutrients and growth regulators occurs via the transpiration stream. The velocity and quantity of water moving from the root to the shoot determines the quantity and concentration of substances that arrive at the shoot. Understanding the forces and resistances that control the movement of water through the soil-plant-air continuum and the flux of potential chemical signals is essential to understanding the impact of the soil environment on root function and on root integration with the shoot.

The objectives of this paper are: a) to discuss the nature of the resistances that limit water flux through the root, b) evaluate methods of measuring root hydraulic conductance, c) describe the effect of temperature and oxygen on root function, and d) discuss the nature of the signals that may be sent from the root to the shoot.

## General principles and definition of terms

Root systems are the rate-limiting site for water movement from the soil to the leaf (Kramer, 1983). This fact is easily demonstrated by taking two wilted tomato plants, placing both in a beaker of water, and excising the root system of one while leaving the other intact. The plant without a root system will regain turgor more rapidly.

Root resistance to water flow is substantial enough to cause low leaf water potentials, even under well-watered conditions. Water potentials of hydroponically grown soybean plants in a growth chamber can reach –0.7 MPa (Markhart et al., 1980). Midday leaf water potentials in well-watered fields can get low enough to cause stomata1 closure and reduce photosynthesis.

We are concerned in this paper with water moving from the root-soil interface to the apoplast of the leaves. Out of necessity, we will divide this pathway into two components. The radial component is from the root-soil interface to the root xylem. The axial component is from the root xylem to the apoplast of the leaf. The flux (Q) through each pathway is determined by the water potential gradient ( $\Delta\psi_w$ ) across the pathway and the conductance (L) of the pathway. If the surface area is known, then the hydraulic conductance can be converted to a hydraulic conductivity (Lp) by dividing L by the surface area.

$$Q = \Delta\psi_w \cdot L \quad [1]$$

The water potential gradient is the difference between the water potential of the soil at the root surface and the water potential of the water in the root xylem. The soil water potential is the sum of the matric potential and the osmotic potential of the soil solution. This quantity is relatively easy to measure. The water potential of the water in the xylem is a different matter. The $\psi_w$ of water in the xylem is the sum of the water potential generated by the pull from transpiration at the shoot and osmotic potential. The latter is generated by the combination of active solute accumulation, passive solute leakage, and rate of water movement from the soil to the xylem. This is difficult, if not impossible, to determine. Conductivity of the radial pathway is determined by structures through which the water flows. Water flows along the path of least resistance. Resistance of the interstices in the cell wall is considered lower than across plasmalemma and cytoplasm. For these reasons, it is thought that water moves apoplasticly across the root until a significant barrier is encountered, at which point the water is forced through the plasmalemma. This apoplastic barrier is the suberin-impregnated endodermal or hypodermal cell wall. Recently, apoplastic movement across the root has been questioned (Steudle and Jeschke, 1983). Using the pressure probe measurements of individual cell Lp and root conductance, they argued that the water moves from cell to cell symplastically and not through the apoplast. Regardless of the exact pathway across the root, at some point, water passes through a highly semipermeable barrier that has characteristics very much like a plasmalemma. In healthy root systems, only 1% of the water either leaks through or bypasses the semipermeability barrier (Hanson et al., 1985).

The casparian band was initially described at the endodermis, but recently has also been described in many plant species as part of a hypodermis located one or two cell layers in from the epidermis (Peterson, 1988). The physical location of the rate-limiting barrier is of considerable interest because it determines where the major potential drop occurs in the transport pathway, and, therefore, the water potential of the different root tissues. For example, if the endodermis is the rate-limiting barrier, then the water potential of the root cortex is close to the water potential of the soil. If, however, the rate-limiting barrier is at the hypodermis, then the water potential of the cortex will be closer to that of the shoot, and, during high transpiration rates, will be much lower than the soil. This aspect could be critical when considering the part of the root sensing the environment and sending chemical messages to the shoot.

The location of the rate-limiting barrier is also important when considering the root-soil interface. A root with an endodermal barrier would undergo less shrinkage during times of high transpiration rate or water deficit than roots with a hypodermal barrier (Passioura, 1988). If roots do shrink under field conditions, a major resistance could occur at the root-soil interface due to poor contact between the root and the liquid phase of the soil solution.

Another important characteristic of the pathway is the ability to accumulate ions actively. At low transpiration rates, this generates an osmotic gradient, driving water into the stele, which is the source of root pressure and guttation. Although we prefer to think of the radial pathway of water movement as a simple pathway, it is important to realize that the pathway is complex, with highly selective barriers and active pumps, with metabolizing cells interacting with a solution pulled through them at varying velocities.

The axial or longitudinal pathway of dead xylem elements connecting the root and the shoot is deceptively simple. Although the conducting elements themselves are dead tubes, they abut xylem parenchyma cells that are metabolically active. In fact, there have been reports of transfer cell-like membrane invaginations (Lauchli, 1976). Whether these cells pump solutes into the xylem or out, or both, is unclear. In any event, it is clear that the concentration and composition of the xylem sap change as it moves up the root.

Published as paper 16993 of scientific journal series of the Minnesota Experiment Station on research conducted under Minnesota Experiment Station Project 0302-4821-82. Additional support was provided by the Univ. of Washington Graduate School Research Fund, Horticultural Research Institute Grant.

### Methods of measuring conductance

*General.* The general principle of measuring root conductance is similar to the measurement of membrane permeability. In a membrane, a chemical potential gradient of the substance of interest is established across the membrane and the flux of the substance is measured. Then, using an equation analogous to Eq. [1], conductance of the membrane is calculated. Conductivity or conductance per unit area can be calculated if the surface area of the membrane is known. Hydraulic conductivity of a root system is measured in a similar fashion. A known water potential difference is established across the root and the water flux through the root system measured. The procedure at first glance is relatively simple. The simplicity, however, stems from a number of assumptions that, in fact, are rarely met. These have been discussed in considerable detail by Fiscus (1975), Dalton et al. (1975), and Newman (1976), but deserve a less quantitative description here.

Water transport is relatively easily measured in roots. Water lost from a reservoir, weight lost from a pot, and transpiration rate measured by gas exchange techniques all work well with whole plants. Detopped root systems give the advantage of being able to measure the flow of exudate from the cut stump.

The major problem is the inability to know adequately the water potential gradient across the membrane or barrier that is limiting water flux. Since the total water potential is composed of a hydrostatic component and an osmotic component, we must know, or be able to estimate reasonably, the hydrostatic potential component and the solute potential on each side of the limiting barrier. The hydrostatic component is straightforward, but the solute potentials are a major problem.

The usual assumption is that the solute potential, acting at the external surface of the limiting barrier, is the same as the external solution and that the solute potential inside the barrier is the same as the exudate emerging from the cut surface of the stump. Unfortunately, neither of these assumptions is very good. Fiscus (1975) has pointed out that, because of the ultrafiltration characteristics of the root, the concentration of solutes at high flow rates at the effective barrier would be significantly higher than that of the ambient solution and the concentration could be less than the ambient at low flow rates if the rate of active transport were greater than the rate of diffusion from the ambient solution to the limiting barrier (Fig. 1).

The concentration inside the limiting barrier also changes considerably with flow due to the combined effects of ultrafiltration and active transport (Fig. 1; see Fig. 3). In addition, the concentration changes as the xylem sap moves toward the shoot (Anderson et al., 1970; Klepper, 1967). Basal portions of the roots of many species actively extract ions from the transpiration stream and either sequester them in the cortex or pump them back out into the ambient solution. In other words, what one measures in the stem xylem is not what is osmotically effective at the osmotically active barrier in the root.

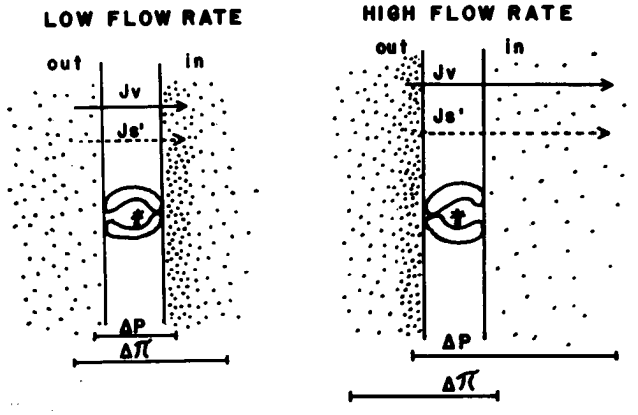


Fig. 1. Large and small hydrostatic potential gradient effects on water flux and osmotic potentials across a semipermeable barrier containing an active solute pump. Jv = total volume flux, Js' = salt flux, Δ P = hydrostatic pressure gradient, and Δ π = osmotic potential gradient. At low transpiration rates the active accumulation of ions (Js') generates an osmotic potential gradient that pulls water into the root. At high transpiration rates, ultrafiltration of the semipermeable barrier results in dilution of the xylem sap in the root and, potentially, an accumulation of solutes outside the barrier. The result is an osmotic gradient that drives water out of the root toward the ambient solution.

### Implications for measuring Lp

The interaction of hydrostatic potential and osmotic potential is most severe at low fluxes. The osmotic potential gradient decreases as the hydrostatic potential gradient increases, resulting in little net change in total water potential driving water movement through a root system. This would not be a problem if one could determine the internal and external osmotic potential and calculate the total water potential gradient accurately. This is, however, impossible. This situation suggests the measurements of Lp using root pressure-generated flow and varying the external solution water potential by the addition of osmoticum are flawed because of the inability to measure the water potential gradient accurately.

The same problem exists for measurements that involve suction applied to the cut stem. The maximum hydrostatic pressure gradient produced by pulling a vacuum is ≈ 70 kPa. This is precisely the range where the interaction of hydrostatic and osmotic driving forces is most pronounced. In other words, a step change in hydrostatic potential gradient results in a smaller-than-expected total water potential change because the osmotic potential changes in the opposite direction to the hydrostatic potential. This problem explains the often-observed curvilinear relationship between hydrostatic potential gradients and flux at low hydrostatic potential gradients.

If the osmotic potential gradient changes substantially relative to the hydrostatic potential gradient and is impossible to measure, then accurate measurements of Lp can only be made over steps in hydrostatic potential where the osmotic potential gradient changes very little. In most root systems this occurs at a hydrostatic potential gradient > 300 kPa. As indicated in Fig. 2, the osmotic potential of the exudate changes very little at this flux, and the flux vs.

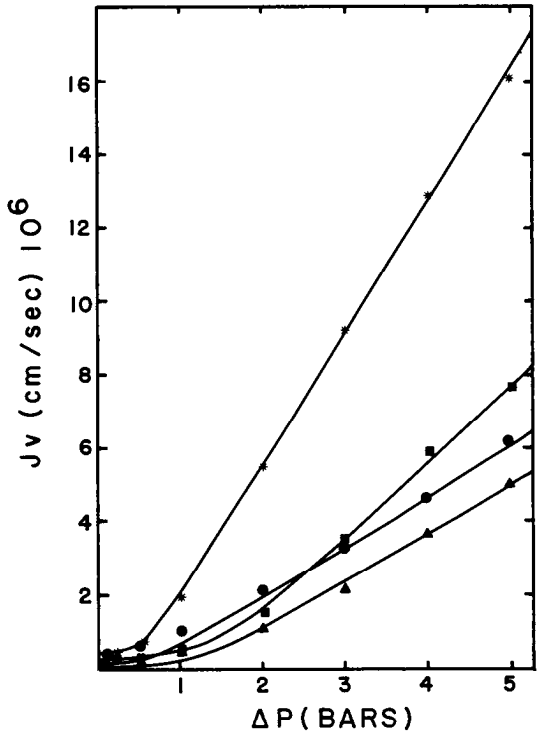


Fig. 2. Relationship between flow rate (Jv) and applied pressure ( Δ P) for de-topped root systems grown and measured in half-strength Hoagland's solution at 25C. Water flux is expressed per unit of root length. (*) soybean Lp = 3.6 E-6 cm·s$^{-1}$·bar$^{-1}$, ( ● ) tomato Lp = 1.37E-6 cm·s$^{-1}$·bar$^{-1}$, ( ▲ ) sunflower Lp = 1.3 E-6 cm·s$^{-1}$·bar$^{-1}$, and ( ■ ) broccoli Lp = 2.1E-6 cm·s$^{-1}$·bar$^{-1}$. (1 bar = 100 kPa).