



Hydraulic resistance of a plant root to water-uptake: A slender-body theory



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HIGHLIGHTS

- An analytical formula for the hydraulic resistance of a single root is derived.
- Local water-uptake profile in the stele is obtained analytically.
- Three-dimensional end effect reduces the hydraulic resistance by as much as 36%.
- Hydraulic resistance is generally not the sum of radial and axial resistances.

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ABSTRACT

A slender-body theory for calculating the hydraulic resistance of a single plant root is developed. The work provides an in-depth discussion on the procedure and the assumptions involved in calculating a root's internal hydraulic resistance as well as the physical and the mathematical aspects of the external three-dimensional flow around the tip of a root in a saturated soil and how this flow pattern enhances uptake and reduces hydraulic resistance. Analytical solutions for the flux density distribution on the stele–cortex interface, local water-uptake profile inside the stele core, the overall water-uptake at the base of the stele, and the total hydraulic resistance of a root are obtained in the slender-body limit. It is shown that a key parameter controlling a root's hydraulic resistance is the dimensionless axial conductivity in the stele, which depends on the permeabilities of the stele and the cortex as well as the root's radial and axial dimensions. Three-dimensional tip effect reduces a root's hydraulic resistance by as much as 36% when compared to the radial flow theory of Landsberg and Fowkes. In addition, the total hydraulic resistance cannot be generally decomposed into the direct sum of a radial resistance and an axial resistance.

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1. Introduction

Water-uptake from soil by a plant's root system is a problem of vital interest to plant biology, agriculture and ecology (Stedle and Peterson, 1998; Stedle, 2000; Raats, 2007; Roose and Schnepf, 2008; Stroock et al., 2014). Significant efforts have been made in the past five decades to quantitatively model water-uptake by a plant's root system, spanning from the mesoscopic single-root scale to the entire root system at the macroscopic scale (Philip, 1957; Gardner, 1960; Cowan, 1965; Landsberg and Fowkes, 1978; Molz, 1981; Passioura, 1988; Stedle, 2000; Raats, 2007; Roose and Schnepf, 2008; Stroock et al., 2014). Various approaches have been used, from considering water flow inside the root structure only (Doussan et al., 1998) to considering water flow in the soil only

(Gardner, 1960; Clausnitzer and Hopmans, 1994), and to the ones that considering simultaneous movement of water in the soil and the root system (Roose and Fowler, 2004; Roose and Schnepf, 2008). At the macroscopic root system level, water-uptake by a plant root is coupled to water transport in an unsaturated soil by the Richard's equation (Raats, 2007)

$$\frac{\partial \theta}{\partial t} = \nabla \cdot [K \nabla p] - S, \quad (1)$$

where θ is the volumetric water content (or relative water saturation; moisture content); $K = K(\theta)$ is the conductivity in the soil which depends on the local water content; p is the water pressure in the soil pores which is also linked to the local water content, $p = p(\theta)$; and S is a volumetric sink term representing root water-uptake. Typical relations for $K(\theta)$ and $p(\theta)$ are given by van Genuchten (1980), for example. The sink term S is also called the water extraction function (Molz, 1981). Since the Richard's Eq. (1)

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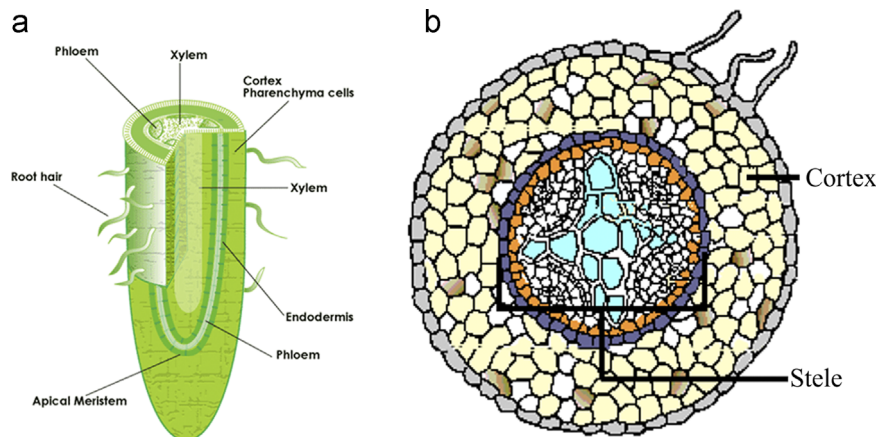


Fig. 1. Typical plant root structure.

describes water transport in the soil at a much larger length scale than the mesoscopic scale of a single rootlet, the sink term S is an uptake averaged over a large number of rootlets (Raats, 2007). S is therefore directly linked to the water-uptake by a single root calculated at the mesoscopic level. Molz (1981) provided a list of various empirical expressions and models for this sink term up to 1981. Raats (2007) discussed in detail a procedure of obtaining the sink term S from the water flow into an individual root, i.e. from a mesoscopic single root model. Volumetric rate of uptake expressed as a sink S in the Richard's equation is at the heart of all macroscopic models; and it must be derived from an analysis of the uptake at the mesoscopic single root scale.

At the mesoscopic scale, a single root has been historically modeled geometrically as a long cylinder with a constant radius, drawing water from the soil in a cylindrical shell (Philip, 1957; Gardner, 1960; Cowan, 1965; Landsberg and Fowkes, 1978; Hainsworth and Aylmore, 1986; Raats, 2007). Inside the root, the water flow in the stele is predominantly longitudinal, and it is controlled by the flow through the xylem tubes (Fig. 1). In the root's cortex and in the soil, water has been modeled to flow only in the radial direction, perpendicular to the cylinder's axis of symmetry. Once the uptake is computed from this simple model for a unit length of the cylindrical root, the volumetric sink term S in the macroscopic Richard's equation is then computed by multiplying the single root uptake by the so-called root length density (Roose and Fowler, 2004; Raats, 2007; Roose and Schnepf, 2008). All of the models for the volumetric sink S discussed in Molz (1981) and Raats (2007) are in fact variations of the original Gardner's two-dimensional radial flow model. However, a two-dimensional radial flow occurs only when the cylinder is infinitely long. Therefore, this widely used model has a serious limitation since all roots have a finite length and the flow around the end of a finite-length cylinder (root) is always three-dimensional. An outcome of neglecting this three-dimensional tip effect is the underestimation of the water flux density on the root-soil surface, which in turn results in an underestimation of the water-uptake by a single root. This point of view is supported by the consideration of the water flow pattern in the soil near a finite-length root shown in Fig. 2 (Chen, 2015). In this example, the finite-length root is geometrically modeled as a slender semi-prolate-spheroid; water in the soil is assumed to be fully saturated and obeys Darcy's law; and the pressure on the root-soil surface is a constant. The mathematical solution for the flow in the soil shown in Fig. 2 is described in Section 4. In Fig. 2, the streamlines of water flow towards the finite-length root clearly show a converging pattern near the tip region of the root. This flow pattern indicates that a significant amount of water enters the root surface from the near

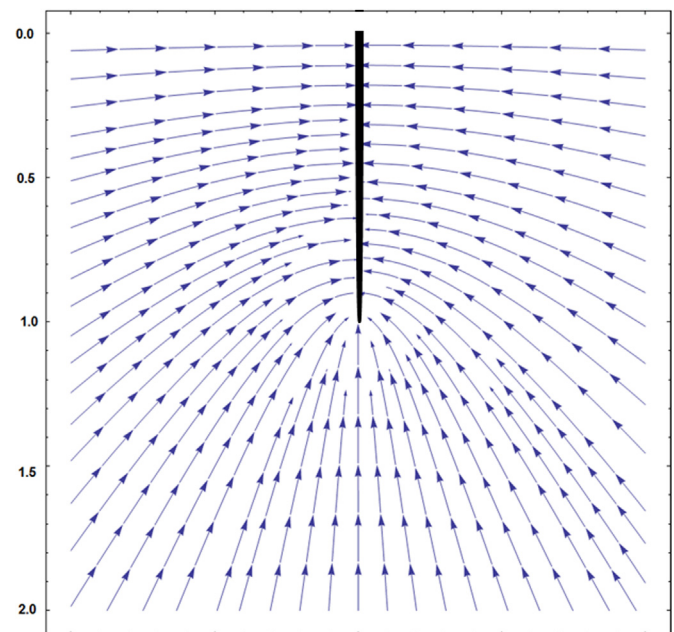


Fig. 2. Streamline patterns of water flow in the soil toward a finite-length root showing the three-dimensional end effect of flow focusing. The streamlines are plotted using the solution given by Eq. (42) in Section 4.

tip region. A similar converging flow pattern also occurs for an unsaturated soil, as the differential operator governing water flow in an unsaturated soil is essentially the same as that for a saturated soil (i.e. Laplacian). Modifications caused by the saturation function do not alter the nature of the differential operator, which controls the process of outward diffusion of the fluid pressure drawdown through the soil. In other words, flow convergence to the root tip is a general phenomenon in both saturated and unsaturated soils. This converging flow pattern, however, cannot be captured by the infinitely long cylinder model which predicts two-dimensional flows with streamlines perpendicular to the root axis; or any other model that ignores the three-dimensional nature of the flow around a root tip.

On the other hand, an argument against the tip effect could be made based on the finding of the "hydraulically isolated" zone near the tip of a root by Frensch and Steudle (1989). Frensch and Steudle (1989) experimentally found that the axial conductivity of the xylem decreases from a constant value to zero within a short distance to the tip. The cone-shaped tip region requires the radius of all xylem vessels to shrink to zero in the region. Therefore, the

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