

# Nutrient Transport Inside and Outside the Root Rhizosphere: Theory<sup>1</sup>

JOHN H. CUSHMAN<sup>2</sup>

## ABSTRACT

The root surface as an absorption mechanism is briefly reviewed and various absorption models are discussed, e.g., the Koshland kinetic and Michaelis-Menten models.

Differences in nutrient availability and transport between the root rhizosphere and bulk soil matrix are examined. The differences manifest themselves in the diffusion coefficients, buffering powers, soil mechanical structure, and nutrient solubility and production. The differences in nutrient transport properties between the rhizosphere and bulk soil matrix are shown to give rise to two coupled partial differential equations. These equations are analytically solved for four sets of boundary conditions. The solutions are used to compute total nutrient uptake by a growing root.

**Additional Index Words:** coupled equations, root absorption, analytical solution.

Cushman, J. H. 1982. Nutrient transport inside and outside the root rhizosphere: theory. *Soil Sci. Soc. Am. J.* 46:704-709.

THE FLOW of nutrients to roots is generally modeled on one of two scales of motion. That is, the root system may be modeled on the macroscopic level in which flow to the bulk root system is studied or, alternatively, on a smaller scale of motion, flow of nutrient to only a single root is examined. In this article we will take the latter approach.

In general, on the root scale of motion the ion uptake rate increases as the external ion concentration increases (see, for example, Fried and Shapiro, 1961). The increase, however, may be in a pseudosaturation fashion (Fig. 1). More often, however, the velocity of absorption vs. concentration plot is just a two-step curve (Nye and Tinker, 1977). In a review article Hodges (1974) proposed an interesting single carrier

model based on the cooperative enzyme kinetics of Koshland (1970) to account for the following three observations: (i) anions are actively pumped inward across the plasmalemma and cations are actively exuded; (ii) the influx of cations and anions exhibit kinetics of the pseudosaturation type discussed above; and (iii) absorption is selective and this selectivity changes with increasing external ion concentration. Unfortunately, Hodges' model is fairly complex and it does not admit a simple mathematical interpretation. Alternatively, it is possible to employ the simpler Michaelis-Menten reaction kinetics to describe the root's absorption capabilities. The Michaelis-Menten kinetic approach has the advantage of being represented by a simple mathematical expression:

$$J_r^j = \frac{J_{\max}^j C_i^j}{Km^j + C_i^j} - E^j, \quad [1]$$

where  $J_{\max}^j$  is the maximum influx,  $Km^j$  is the value of the concentration at which  $J_r^j = J_{\max}^j/2$ ,  $J_r^j$  is the influx of the  $j^{\text{th}}$  species (Epstein and Hagen, 1952),

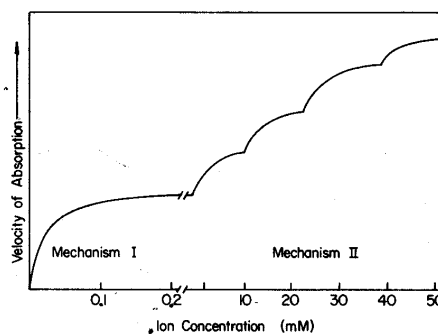


Fig. 1—Velocity of ion influx into roots as a function of external ion concentration (after Hodges, 1974).

<sup>1</sup> Contribution from the Purdue Agric. Exp. Stn., W. Lafayette, Ind., Journal Paper no. 8789. Received 3 Nov. 1981. Approved 10 Mar. 1982.

<sup>2</sup> Associate Professor of Soil Physics, Purdue University.

$E^j$  is the efflux (considered to be constant), and  $C_l^j$  is the  $j^{\text{th}}$  species concentration in liquid phase.

Prior to the nutrients being positionally available at the root surface for absorption, they in general are transported to the root through the root rhizosphere. The root rhizosphere is the region immediately next to the root surface extending out to a distance of about 4 mm (Hiltner, 1904) from the root surface. The root rhizosphere consists of five overlapping categories of compounds (Rovira et al., 1979):

1. *Exudates*—nonmetabolically released compounds of low molecular weight which leak from cells in the soil by either intercellular spaces or through epidermal walls.
2. *Secretions*—compounds of both low and high molecular weight mucilages which are released as a result of metabolic processes.
3. *Plant mucilages*—there are basically four types: (i) root cap mucilage, (ii) hydrolysates of the polysaccharide of the primary cell wall between epidermal cells and sloughed root cap cells, (iii) mucilage secreted by the epidermal cells which still only have primary walls (including mucilage from root hairs), and (iv) mucilage produced by bacterial degradation of the outer-lamella primary cell walls of old, dead epidermal cells.
4. *Mucigel*—the gelatinous material at the root surface grown in normal nonsterile soils (including natural and modified plant mucilages, bacterial cells, and their metabolic products as well as colloidal, mineral, and organic matter from the soil).
5. *Lysates*—compounds released from autolysis of older epidermal cells when the plasmalemma fails.

It is interesting to consider the contact the root makes with the soil matrix. In general, the outer epidermal surface of a young root is covered with a mucilage and hence not in direct contact with the soil (Oades, 1978). The mucilage combines with the soil colloids and organic matter to form a mucigel. Both water and ions are able to diffuse through this mucigel (Greenland, 1979). Moreover, this author believes that convective flux of water also exists in the mucigel. Evidence supporting this conjecture is that convection of water in clay pastes can take place (see, for example, Mokady and Low, 1968; Banin and Low, 1971).

The pectin component of the mucigel readily binds cations, and hence before the Casparian band on the endodermal cell is formed, it may retard some heavy metal cations from entering young roots (Barlow, 1975).

Kept et al. (1979) have suggested that there are three mechanisms by which availability of phosphates is affected in the rhizosphere: (i) release of phosphate from insoluble phosphates (Ca, Al, Fe) may be increased by the formation of soluble complexes between metal ions and metabolites; (ii) organic acids found in root exudates capable of forming adsorption complexes (e.g., chelates) compete for phosphate adsorbed on kaolinite and aluminum oxides; and (iii) when cation absorption into the root exceeds anion absorption, the rhizosphere pH falls, and similarly

hydration of  $\text{CO}_2$  to carbonic acid and release of cellular organic acids may alter the pH.

Root hairs in the rhizosphere make nutrients with small diffusion coefficients more accessible to the plant. However, an even larger effect may be induced by mycorrhizal fungi (see, for example, Owusu-Benoah and Wild, 1979). Endotrophic and ectotrophic mycorrhiza hyphae extend for distances much larger than those of root hairs. It is not true that microorganisms always have a positive effect on ion uptake, however (Hale and Moore, 1979).

For the longer growing periods or for the more mobile nutrients, it is possible for ions to be transported to the rhizosphere from the external soil matrix. There are five basic dynamic mechanisms which control the flow of nutrients outside the root rhizosphere (Cushman, 1981): (i) solution phase diffusion; (ii) surface phase diffusion; (iii) convection; (iv) mechanical dispersion; and (v) solid-liquid exchange phenomena. These mechanisms also exist in the rhizosphere. However, one should add to this list a sixth mechanism in the rhizosphere: (vi) microbial and other induced solute changes (for example, as we've already mentioned, the three factors of Kept et al., 1979).

#### STATEMENT OF THE TRANSPORT PROBLEM

What I would like to do now is write down a tractable mathematical representation of nutrient flow to the root both inside and outside the root rhizosphere.

Consider Fig. 2, which is a simplified representation of a root surrounded by its rhizosphere which in turn is surrounded by the undisturbed soil matrix. We make the simplifying assumptions that in Region I the soil is isotropic and homogeneous while in Region II we also have isotropy and homogeneity. However, we do not stipulate that Regions I and II combined form a homogeneous region (e.g., Region I may have a higher bulk density than Region II, or Region I may contain gels, whereas Region II will not). So that the flow problem may be represented one dimensionally, we assume the root is cylindrical and the concentration gradients along the root axis are small compared with the radial gradients. Moreover, we will assume constant moisture conditions, Darcy velocity (as can be maintained in a laboratory study), and effective

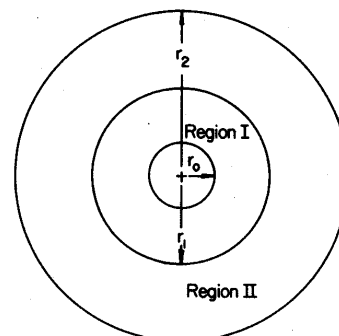


Fig. 2—A simplified representation of the root, root rhizosphere, and external soil matrix. The parameters  $r_0$ ,  $r_1$ , and  $r_2$  are, respectively, the root radius, rhizosphere radius, and external radius of influence of the root.

diffusion coefficient. We also have the ions moving on a concentration gradient as a first approximation to the true free energy gradient. With these assumptions, the radial flux ( $J$ ) of a given species in region  $i$  is given by (Nye and Marriott, 1969):

$$J^{(i)} = b^{(i)} D^{(i)} [\partial C_i^{(i)} / \partial r] + v C_i^{(i)}, \quad [2]$$

where  $b$  is the buffer power (assumed constant),  $D$  is the effective diffusion coefficient (Cushman, 1981),  $C_i$  is the solution phase concentration, and  $v$  is the transpiration-induced convective velocity of the water.

Using the assumptions of Cushman (1980a) we may derive the following equation for flow in the rhizosphere:

$$\frac{\partial C_i^{(1)}}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left( r D^{(1)} \frac{\partial C_i^{(1)}}{\partial r} + \frac{v_o r_o}{b^{(1)}} C_i^{(1)} \right) + \frac{\alpha}{b^{(1)}}, \quad [3]$$

$$t > 0, r_o < r < r_1,$$

where  $\alpha$  is the mass of solute in soil solution produced or depleted per unit time per unit volume in the rhizosphere,  $v_o$  and  $r_o$  are, respectively, the velocity of water at the root surface and the root radius, and  $r_1$  is the radius of the outer edge of the rhizosphere.

If we assume there is negligible production or depletion of nutrient outside the rhizosphere, then we have (Cushman, 1979):

$$\frac{\partial C_i^{(2)}}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left( r D^{(2)} \frac{\partial C_i^{(2)}}{\partial r} + \frac{v_o r_o}{b^{(2)}} C_i^{(2)} \right), \quad [4]$$

$$t > 0, r_1 < r < r_2,$$

where  $r_2$  is some outer radius of influence of the root. We thus have two equations coupled by boundary conditions which must be solved simultaneously subject to appropriate initial conditions. The appropriate boundary condition at the root surface is found by setting Eq. [1] equal to Eq. [2] at  $r = r_o$  to give:

$$D^{(1)} b^{(1)} \frac{\partial C_i^{(1)}}{\partial r} + v_o C_i^{(1)} = \frac{k C_i^{(1)}}{1 + k C_i^{(1)} / J_{\max}} - E, \quad [5]$$

$$t > 0, r = r_o,$$

where  $k = J_{\max} / K_m$  is called the root absorption power. If we assume the concentration in solution is low, then Eq. [5] reduces to:

$$D^{(1)} b^{(1)} [\partial C_i^{(1)} / \partial r] + v_o C_i^{(1)} = k C_i^{(1)} - E, \quad [6]$$

$$t > 0, r = r_o,$$

or, if we assume  $C_i$  is high, then Eq. [5] reduces to:

$$D^{(1)} b^{(1)} [\partial C_i^{(1)} / \partial r] + v_o C_i^{(1)} = J_{\max} - E, \quad [7]$$

$$t > 0, r = r_o.$$

There are two boundary conditions at  $r_1$ . The first is that the concentration in solution profile is continuous, i.e.:

$$C_i^{(1)} = C_i^{(2)}, t > 0, r = r_1, \quad [8]$$

and the second is that we have continuity of total flux:

$$v_1 C_i^{(1)} + D^{(1)} b^{(1)} [\partial C_i^{(1)} / \partial r] = v_1 C_i^{(2)} + D^{(2)} b^{(2)} [\partial C_i^{(2)} / \partial r], \quad [9]$$

$$t > 0, r = r_1$$

or using Eq. [8] in Eq. [9]:

$$\frac{\partial C_i^{(1)}}{\partial r} = \frac{D^{(2)} b^{(2)}}{D^{(1)} b^{(1)}} \frac{\partial C_i^{(2)}}{\partial r}, t > 0, r = r_1, \quad [10]$$

where  $v_1$  is the velocity of water at  $r = r_1$ .

We will consider two different boundary conditions at the outer radius of influence ( $r_2$ ) of the root. First, there is the possibility of no nutrient replenishment at  $r_2$  due to inter-root competition, (Cushman, 1979):

$$D^{(2)} b^{(2)} \frac{\partial C_i^{(2)}}{\partial r} + \frac{r_o}{r_2} v_o C_i^{(2)} = 0, t > 0, r = r_2; \quad [11]$$

and second, there is the case when there is no competition:

$$C_i^{(2)} = C_i, t > 0, r = r_2, \quad [12]$$

where  $C_i$  is the initial concentration in the solution phase.

For an initial condition we will assume an everywhere constant concentration in the solution phase:

$$C_i^{(2)} = C_i^{(1)} = C_i, t = 0. \quad [13]$$

If we assume that  $\alpha$  is constant, we may introduce the following list of nondimensional variables into the equations of flow:

$$\eta^{(j)} = t(D^{(j)} / r_o^2), \quad \mu = r / r_o, \quad \rho = k C_i / J_{\max}, \quad \theta^{(j)} = 1 - C_i^{(j)} / C_i, \quad d = E / k C_i, \quad Q = -\alpha r_o^2 / b^{(1)} C_i D^{(1)}, \quad \lambda = D^{(1)} / D^{(2)}, \quad \tau = k / v_o,$$

and

$$a^{(j)} = r_j / r_o.$$

With these nondimensional variables, we set up two problems that must be solved simultaneously:

### 1. Problem I (Region I)

#### a. Main Equation:

$$\frac{\partial \Theta^{(1)}}{\partial \eta^{(1)}} = \frac{\partial^2 \Theta^{(1)}}{\partial \mu^2} + \frac{1}{\mu} (1 - 2\nu^{(1)}) \frac{\partial \Theta^{(1)}}{\partial \mu} + Q^{(1)}, \quad [14]$$

$$\eta^{(1)} > 0, 1 < \mu < a^{(1)},$$

b. Boundary conditions [ $\beta^{(1)}$  and  $\Gamma^{(1)}$  are defined immediately following the statement of the B.C.]:

$$\partial \Theta^{(1)} / \partial \mu = \beta^{(1)} \Theta^{(1)} + \Gamma^{(1)}, \eta^{(1)} > 0, \mu = 1. \quad [15]$$

If there is a linear uptake rate,

$$\beta^{(1)} = 2\nu^{(1)}(1 - \tau) \quad \text{and} \quad \Gamma^{(1)} = -2\nu^{(1)}[1 + (d - 1)\tau].$$

If there is constant uptake rate,

$$\beta^{(1)} = 2\nu^{(1)} \quad \text{and} \quad \Gamma^{(1)} = 2\nu^{(1)}(\tau/\rho - d\tau - 1). \quad [16]$$

$$\Theta^{(1)} = \Theta^{(2)}, \eta^{(1)} = \lambda\eta^{(2)} > 0, \mu = a^{(1)}, \quad [16]$$

$$\frac{\partial\Theta^{(1)}}{\partial\mu} = \frac{\nu^{(1)}}{\nu^{(2)}} \frac{\partial\Theta^{(2)}}{\partial\mu}, \eta^{(1)} = \lambda\eta^{(2)} > 0, \mu = a^{(1)}, \quad [17]$$

c. Initial condition:

$$\Theta^{(1)} = 0, 1 \leq \mu \leq a^{(1)}, \eta^{(1)} = 0. \quad [18]$$

## 2. Problem II (Region II)

a. Main equation:

$$\frac{\partial\Theta^{(2)}}{\partial\eta^{(2)}} = \frac{\partial^2\Theta^{(2)}}{\partial\mu^2} + \frac{1}{\mu}[1 - 2\nu^{(2)}] \frac{\partial\Theta^{(2)}}{\partial\mu}, \quad [19]$$

$$\eta^{(2)} > 0, a^{(1)} < \mu < a^{(2)},$$

b. Boundary conditions  $[\beta^{(2)}]$  and  $\Gamma^{(2)}$  are defined immediately following the statement of the B.C.:

$$\mathcal{A} \frac{\partial\Theta^{(2)}}{\partial\mu} = \beta^{(2)}\Theta^{(2)} + \Gamma^{(2)}, \eta^{(2)} > 0, \mu = a^{(2)}. \quad [20]$$

If there is interroot competition,

$$\mathcal{A} = 1, \beta^{(2)} = 2\nu^{(2)}/a^{(2)}, \quad \text{and} \quad \Gamma^{(2)} = -[2\nu^{(2)}/a^{(2)}].$$

If there is no interroot competition,

$$\mathcal{A} = 0, \beta^{(2)} = 1, \quad \text{and} \quad \Gamma^{(2)} = 0.$$

We also have Eq. [16] and Eq. [17] holding as boundary conditions.

c. Initial condition:

$$\Theta^{(2)} = 0, a^{(1)} \leq \mu \leq a^{(2)}, \eta^{(2)} = 0. \quad [21]$$

## SOLUTION TO THE TRANSPORT PROBLEM

Since the equations of flow established in the last section are linear they are amenable to analytical solution techniques. In particular we will follow and generalize the solution procedure presented in Cushman (1979, 1980a).

Consider Problem I first and let

$$\Theta^{(1)}(\mu, \eta^{(1)}) = f(\mu) + g(\mu, \eta^{(1)}), \quad [22]$$

so that Eq. [14] and Eq. [15] reduce to

$$0 = f'' + \frac{1}{\mu}(1 - 2\nu^{(1)})f' + Q, \quad [22a]$$

$$\dot{g} = g'' + \frac{1}{\mu}(1 - 2\nu^{(1)})g'$$

where

$$\dot{g} = \frac{\partial g}{\partial\eta^{(1)}}, g' = \frac{\partial g}{\partial\mu}, \quad [22b]$$

and

$$f' = \beta^{(1)}f + \Gamma^{(1)}, \mu = 1, \eta^{(1)} > 0, \quad [23a]$$

$$g' = \beta^{(1)}g, \mu = 1, \eta^{(1)} > 0. \quad [23b]$$

We also set  $f = 0$  at  $\mu = a^{(1)}, \eta^{(1)} > 0$  so that  $\Theta^{(1)} = g = \Theta^{(2)}$  at  $\mu = a^{(1)}, \eta^{(1)} > 0$ .

The general solutions to Eq. [22a] and Eq. [22b] are:

$$f(\mu) = \frac{E^{(1)}}{2\nu^{(1)}\mu^{2\nu^{(1)}}} - \frac{Q}{4(1 - \nu^{(1)})\mu^2} + F^{(1)}, \quad [24a]$$

$$g(\mu, \eta^{(1)}) = \mu^{\nu^{(1)}}\{A^{(1)}J_{\nu^{(1)}}[\alpha^{(1)}\mu] + B^{(1)}Y_{\nu^{(1)}}[\alpha^{(1)}\mu]\} \exp[-(\alpha^{(1)})^2\eta^{(1)}] + C^{(1)}\mu^{2\nu^{(1)}} + D^{(1)}, \quad [24b]$$

where  $E^{(1)}, F^{(1)}, A^{(1)}, \alpha^{(1)}, B^{(1)}, C^{(1)}$ , and  $D^{(1)}$  are arbitrary constants and  $J_\nu$  and  $Y_\nu$  are Bessel functions of order  $\nu$  of the first and second kind. Insertion of Eq. [23a, b] into Eq. [24a, b] and recalling  $f(a^{(1)}) = 0$  gives:

$$\begin{aligned} \Theta^{(1)}[\mu, \eta^{(1)}] = & A^{(1)}\mu^{\nu^{(1)}}\{[\alpha^{(1)}Y_{\nu^{(1)}-1}(\alpha^{(1)}) \\ & - \beta^{(1)}Y_{\nu^{(1)}}(\alpha^{(1)})]J_{\nu^{(1)}}(\alpha^{(1)}\mu) - [\alpha^{(1)}J_{\nu^{(1)}-1}(\alpha^{(1)}) \\ & - \beta^{(1)}J_{\nu^{(1)}}(\alpha^{(1)})]Y_{\nu^{(1)}}(\alpha^{(1)}\mu)\} \exp[-(\alpha^{(1)})^2\eta^{(1)}] \\ & + C^{(1)}\left[\mu^{2\nu^{(1)}} + \frac{2\nu^{(1)} - \beta^{(1)}}{\beta^{(1)}}\right] \\ & + \frac{Q}{4(1 - \nu^{(1)})}[\beta^{(1)}(a^{(1)})^2 - \beta^{(1)} + 2] + \Gamma^{(1)} \\ & + \frac{2\nu^{(1)} + \beta^{(1)}[(a^{(1)})^{2\nu^{(1)}} - 1]}{2\nu^{(1)} + \beta^{(1)}[(a^{(1)})^{2\nu^{(1)}} - 1]}\mu^{2\nu^{(1)}} \\ & - \frac{Q}{4(1 - \nu^{(1)})}\mu^2 \\ & + \frac{Q}{4(1 - \nu^{(1)})}[(2\nu^{(1)} - \beta^{(1)})(a^{(1)})^2 + (\beta^{(1)} - 2)(a^{(1)})^{2\nu^{(1)}}] \\ & + \frac{2\nu^{(1)} + \beta^{(1)}[(a^{(1)})^{2\nu^{(1)}} - 1]}{2\nu^{(1)} + \beta^{(1)}[(a^{(1)})^{2\nu^{(1)}} - 1]} \\ & + \frac{\Gamma^{(1)}(a^{(1)})^{2\nu^{(1)}}}{2\nu^{(1)} + \beta^{(1)}[(a^{(1)})^{2\nu^{(1)}} - 1]}. \end{aligned} \quad [25]$$

Similarly, the general solution to Eq. [19] that satisfies Eq. [20] is as follows:

$$\begin{aligned} \Theta^{(2)}(\mu, \eta^{(2)}) = & A^{(2)}\mu^{\nu^{(2)}}\{[\mathcal{A}\alpha^{(2)}Y_{\nu^{(2)}-1}(\alpha^{(2)}a^{(2)}) \\ & - \beta^{(2)}Y_{\nu^{(2)}}(\alpha^{(2)}a^{(2)})]J_{\nu^{(2)}}(\alpha^{(2)}\mu) \\ & - [\mathcal{A}\alpha^{(2)}J_{\nu^{(2)}-1}(\alpha^{(2)}a^{(2)}) \\ & - \beta^{(2)}J_{\nu^{(2)}}(\alpha^{(2)}a^{(2)})]Y_{\nu^{(2)}}(\alpha^{(2)}\mu)\} \exp[-(\alpha^{(2)})^2\eta^{(2)}] \\ & + C^{(2)}\left[\mu^{2\nu^{(2)}} + \frac{(\mathcal{A}2\nu^{(2)}(a^{(2)})^{2\nu^{(2)}-1} - \beta^{(2)}a^{2\nu^{(2)}})}{\beta^{(2)}}\right] - \frac{\Gamma^{(2)}}{\beta^{(2)}}, \end{aligned} \quad [26]$$

where  $A^{(2)}, \alpha^{(2)}$ , and  $C^{(2)}$  are arbitrary constants. So that we may evaluate conditions [16] and [17] we set  $\alpha^{(2)} = \alpha^{(1)}\sqrt{\lambda}$  giving:

$$\begin{aligned} \exp[(\alpha^{(2)})^2\eta^{(2)}] &= \exp[(\alpha^{(1)})^2\lambda\eta^{(2)}] \\ &= \exp[(\alpha^{(1)})^2\eta^{(1)}] = \exp[\alpha^2\eta], \end{aligned} \quad [27]$$

where we have set  $\alpha = \alpha^{(1)}$  and  $\eta = \eta^{(1)}$ .

The next logical step is to insert condition [16] followed by condition [17] to give the

$$\begin{aligned}
\Theta(\mu, \eta) = & \sum_{n=1}^{\infty} A_n \left\langle \chi_{[1, a^{(1)}]}(\mu) \mu^{\nu^{(1)}} (a^{(1)})^{\nu^{(2)}} \right. \\
& \{ [\mathcal{A} \alpha_n \sqrt{\lambda} Y_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(1)}) \\
& - [\mathcal{A} \alpha_n \sqrt{\lambda} J_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(1)}) \} \{ [\alpha_n Y_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} Y_{\nu^{(1)}}(\alpha_n)] J_{\nu^{(1)}}(\alpha_n \mu) - [\alpha_n J_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} J_{\nu^{(1)}}(\alpha_n)] Y_{\nu^{(1)}}(\alpha_n \mu) \} \\
& + \chi_{[a^{(1)}, a^{(2)}]}(\mu) \mu^{\nu^{(2)}} (a^{(1)})^{\nu^{(1)}} \{ [\alpha_n Y_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} Y_{\nu^{(1)}}(\alpha_n)] J_{\nu^{(1)}}(\alpha_n a^{(1)}) - [\alpha_n J_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} J_{\nu^{(1)}}(\alpha_n)] Y_{\nu^{(1)}}(\alpha_n a^{(1)}) \} \\
& \{ [\mathcal{A} \alpha_n \sqrt{\lambda} Y_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} \mu) \\
& - [\mathcal{A} \alpha_n \sqrt{\lambda} J_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} \mu) \} \rangle \exp[-\alpha_n^2 \eta] \\
& + \chi_{[1, a^{(1)}]}(\mu) \left[ C \left( \mu^{2\nu^{(1)}} + \frac{2\nu^{(1)} - \beta^{(1)}}{\beta^{(1)}} \right) \right. \\
& + E_0 \mu^{2\nu^{(1)}} + E_1 \mu^2 + E_2 \left. \right] \\
& + \chi_{[a_1, a_2]}(\mu) \left\langle \left[ C \left[ (a^{(1)})^{2\nu^{(1)}} + \frac{2\nu^{(1)} - \beta^{(1)}}{\beta^{(1)}} \right] + E_0 (a^{(1)})^{2\nu^{(1)}} \right. \right. \\
& + E_1 (a^{(1)})^2 + E_2 + \frac{\Gamma^{(2)}}{\beta^{(2)}} \left. \right\} \cdot \{ \mu^{2\nu^{(2)}} + E_3 \} / \\
& \{ (a^{(1)})^{2\nu^{(2)}} + E_3 \} - \frac{\Gamma^{(2)}}{\beta^{(2)}} \left. \right\rangle, \quad [28]
\end{aligned}$$

where

$$\begin{aligned}
E_3 &= \frac{\mathcal{A} 2\nu^{(2)} (a^{(2)})^{2\nu^{(2)}-1} - \beta^{(2)} (a^{(2)})^{2\nu^{(2)}}}{\beta^{(2)}}, \\
E_2 &= \frac{(\beta^{(1)} - 2\nu^{(1)}) E_1 (a^{(1)})^2 - [(\beta^{(1)} - 2) E_1 + \Gamma^{(1)}] (a^{(1)})^{2\nu^{(1)}}}{2\nu^{(1)} - \beta^{(1)} [1 - (a^{(1)})^{2\nu^{(1)}}]}, \\
E_1 &= -\frac{Q}{4(1 - \nu^{(1)})}, \\
E_0 &= \frac{(\beta^{(1)} - 2) E_1 + \Gamma^{(1)} - \beta^{(1)} E_1 (a^{(1)})^2}{2\nu^{(1)} - \beta^{(1)} [1 - (a^{(1)})^{2\nu^{(1)}}]}, \\
C &= \left\langle -2\nu^{(1)} E_0 (a^{(1)})^{2\nu^{(1)}-1} - 2E_1 a^{(1)} \right. \\
& + 2\nu^{(1)} (a^{(1)})^{2\nu^{(2)}-1} \left[ E_0 (a^{(1)})^{2\nu^{(1)}} + E_1 (a^{(1)})^2 + E_2 \right. \\
& + \frac{\Gamma^{(2)}}{\beta^{(2)}} \left. \right] / [(a^{(1)})^{2\nu^{(2)}} + E_3] \left. \right\rangle / \left\{ 2\nu^{(1)} (a^{(1)})^{2\nu^{(1)}-1} \right. \\
& - 2\nu^{(1)} (a^{(1)})^{2\nu^{(2)}-1} \left[ (a^{(1)})^{2\nu^{(1)}} + \frac{2\nu^{(1)} - \beta^{(1)}}{\beta^{(1)}} \right] / [(a^{(1)})^{2\nu^{(2)}} + E_3] \left. \right\},
\end{aligned}$$

$\chi_A(\mu)$  is the characteristic (indicator) function of the set  $A$ , the  $\alpha_n$  are the roots of

$$\begin{aligned}
O = & \{ [\mathcal{A} \alpha_n \sqrt{\lambda} Y_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(1)}) \\
& - [\mathcal{A} \alpha_n \sqrt{\lambda} J_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(1)}) \} \\
& \cdot \{ [\alpha_n Y_{\nu^{(1)}-1}(\alpha_n) - \beta^{(1)} Y_{\nu^{(1)}}(\alpha_n)] J_{\nu^{(1)}}(\alpha_n a^{(1)}) \\
& - [\alpha_n J_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} J_{\nu^{(1)}}(\alpha_n)] Y_{\nu^{(1)}}(\alpha_n a^{(1)}) \} - \frac{\nu^{(1)}}{\nu^{(2)}} \{ [\alpha_n Y_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} Y_{\nu^{(1)}}(\alpha_n)] J_{\nu^{(1)}}(\alpha_n a^{(1)}) - [\alpha_n J_{\nu^{(1)}-1}(\alpha_n) \\
& - \beta^{(1)} J_{\nu^{(1)}}(\alpha_n)] Y_{\nu^{(1)}}(\alpha_n a^{(1)}) \} \{ [\mathcal{A} \alpha_n \sqrt{\lambda} Y_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] J_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(1)}) \\
& - [\mathcal{A} \alpha_n \sqrt{\lambda} J_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\
& - \beta^{(2)} J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] Y_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(1)}) \},
\end{aligned}$$

and the  $A_n$  are determined by the modified Gram-Schmidt method (Kirkham and Powers, 1972).

#### TOTAL NUTRIENT UPTAKE

Using the solution developed in the last section it is possible to construct an analytical representation of the total nutrient absorbed by a growing root. In particular, if we make the assumption that the roots are growing strictly parallel to the root axis, at a rate such that the flux parallel to the root axis is negligible compared to the radial flux, then we can use the Cushman (1979) equation for total uptake:

$$\begin{aligned}
T = & 2\pi r_o L_o \int_0^{t_{\max}} F(s) ds \\
& + 2\pi r_o \int_0^{t_{\max}} \frac{dg}{dt} \int_0^{t_{\max}-t} F(s) ds dt. \quad [29]
\end{aligned}$$

The parameters in the above equation are total uptake ( $T$  which is computed from  $t = 0$  to  $t = t_{\max}$ ), initial root length [ $g(0) = L_o$ ], and flux of nutrient at the root surface [ $F(t)$ ]. We also assume the root grows at the rate  $g(t)$ . If we assume the roots are young and growing at the exponential rate,

$$g(t) = L_o \exp(\gamma t) \quad [30]$$

then we may follow Cushman (1979) and define a non-dimensional uptake as follows:

$$T_N = \frac{D^{(1)}}{2\pi r_o^3 k C_i L_o} T,$$

where  $T$  can be written

$$T = \frac{2\pi r_o^3 k C_i L_o}{D^{(1)}} \left\{ \int_0^{\eta_{\max}} [1 - \Theta(1, \eta) - d] d\eta \right\}$$

$$+ \psi \int_0^{\eta_{\max}} \exp(\psi\eta) \int_0^{\eta_{\max}-\eta} [1 - \Theta(1, s) - d] ds d\eta \}, [31]$$

and  $\psi\eta = t\gamma$ .

We next define

$$P(x, y, z) = [\exp(xy) - \exp(-zy)] \left( 1 - \frac{x}{x+z} \right) / z, [32]$$

and

$$Q(x, y) = [\exp(xy) - 1]/x. [33]$$

Using Eq. [32] and Eq. [33] we may write down the closed-form nondimensional total nutrient uptake as follows:

$$\begin{aligned} T_N = & - \sum_{n=1}^{\infty} A_n (\alpha_n^{(1)})^{\nu^{(2)}} \{ [\alpha_n \sqrt{\lambda} Y_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\ & - \beta^{(2)} Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(1)}) \\ & - [\alpha_n \sqrt{\lambda} J_{\nu^{(2)}-1}(\alpha_n \sqrt{\lambda} a^{(2)}) \\ & - \beta^{(2)} J_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(2)})] Y_{\nu^{(2)}}(\alpha_n \sqrt{\lambda} a^{(1)}) \} \\ & \{ [\alpha_n Y_{\nu^{(1)}-1}(\alpha_n) \\ & - \beta^{(1)} Y_{\nu^{(1)}}(\alpha_n)] J_{\nu^{(1)}}(\alpha_n) - [\alpha_n J_{\nu^{(1)}-1}(\alpha_n) \\ & - \beta^{(1)} J_{\nu^{(1)}}(\alpha_n)] Y_{\nu^{(1)}}(\alpha_n) \} P(\psi, \eta_{\max}, \alpha_n^2) \\ & + \left[ 1 - d - C \left( 1 + \frac{2\nu^{(1)} - \beta^{(1)}}{\beta^{(1)}} \right) \right. \\ & \left. - E_0 - E_1 - E_2 \right] Q(\psi, \eta_{\max}). [34] \end{aligned}$$

Although Eq. [34] holds for both high and low nutrient contents in soil solution, a simpler equation exists for the case where the nutrient content in solution is high (Cushman, 1980b):

$$T_N^h = \exp(\psi\eta_{\max}) - 1, [35]$$

and

$$T^h = 2\pi r_o L_o (J_{\max} - E) \frac{1}{\gamma} [\exp(\psi\eta_{\max}) - 1]. [36]$$

### DISCUSSION

Transport and availability of nutrient between the inside and the outside of the root rhizosphere may be substantially different. The difference arises from the differing coefficients of transport and the varying nutrient productivity rates. We have presented a system of two coupled equations and four sets of boundary conditions to represent the differing flow mechanisms inside and outside the rhizosphere. The equations were nondimensionalized and solved via use of an infinite series of Bessel functions and the modified Gram-Schmidt procedure. The analytical concentration equation was evaluated at the root surface and substituted into an equation representing total nutrient uptake for a root growing at an exponential rate. In this fashion we are able to give a closed form exact description of the cumulative nutrient uptake.

In the second of this sequence of two articles I will examine the general Michaelis-Menton boundary condition, present a numerical algorithm for the solution to the nonlinear problem, present detailed graphical results for the equations developed in this article as a function of the numerous possible parameter values, compare the nonlinear to the linear solutions, examine a nonlinear production term, and draw overall conclusions concerning the analytical effect of the rhizosphere on nutrient uptake.

### ACKNOWLEDGMENTS

Support for this project has been drawn from the "Purdue Onsite Waste Disposal Project."

### REFERENCES

1. Banin, A., and P. F. Low. 1971. Simultaneous transport of water and salt through clays: 2. Steady-state distribution of pressure and applicability of irreversible thermodynamics. *Soil Sci.* 112:69-88.
2. Barlow, P. W. 1975. The root cap. p. 21. In J. G. Torrey and D. T. Clarkson (ed.) *The development and function of roots*. Academic Press, London.
3. Cushman, J. H. 1979. An analytical solution for solute transport near root surfaces for low initial concentration: I. Equations development. *Soil Sci. Soc. Am. J.* 43:1087-1090.
4. Cushman, J. H. 1980a. Analytical study of the effect of ion depletion (replenishment) caused by microbial activity near a root. *Soil Sci.* 129:69-87.
5. Cushman, J. H. 1980b. Completion of the list of analytical solutions for nutrient transport to roots: 1. Exact linear models. *Water Resour. Res.* 16:891-906.
6. Cushman, J. H. 1982. Incorporation of the rhizosphere into plant root models. In D. W. Nelson et al. (ed.) *Chemical mobility and reactivity in soil systems* (in preparation). Special Pub. American Society of Agronomy, Madison, Wis.
7. Epstein, E., and C. E. Hagen. 1952. A kinetic study of the absorption of alkali cations by barley roots. *Plant Physiol.* 27:457-474.
8. Fried, M., and R. E. Shapiro. 1961. Soil-plant relationships in ion uptake. *Annu. Rev. Plant Physiol.* 12:91-112.
9. Greenland, D. J. 1979. The physics and chemistry of the soil root interface: some comments. p. 83-97. In S. L. Harley and R. S. Russell (ed.) *The soil root interface*. Academic Press, New York.
10. Hale, H. G., and L. D. Moore. 1979. Factors affecting root exudation: II. 1970-1978. *Adv. Agron.* 31:93-124.
11. Hiltner, L. 1904. *Arbeiten der Deutschen. Landwirtschaft. Ges.* 98:59-78.
12. Hodges, T. K. 1974. Ion absorption by plant roots. *Adv. Agron.* 25:163-207.
13. Kepert, D. G., A. D. Robson, and A. M. Posner. 1979. The effect of organic root products on the availability of phosphorus to plants. p. 115-124. In J. L. Harley and R. S. Russell (ed.) *The soil root interface*. Academic Press, New York.
14. Kirkham, D., and W. L. Powers. 1972. *Advanced soil physics*. John Wiley & Sons, New York.
15. Koshland, D. E. 1970. p. 341-396. In P. D. Boyer (ed.) *The enzymes*. (3rd ed.) Vol. 1. Academic Press, New York.
16. Mokady, R. S., and P. F. Low. 1968. Simultaneous transport of water and salt through clays: I. Transport mechanisms. *Soil Sci.* 105:112-131.
17. Nye, P. H., and F. H. C. Marriott. 1969. Theoretical study of the distribution of substances around roots resulting from simultaneous diffusion and mass flow. *Plant Soil* 3:459-472.
18. Nye, P. H., and P. B. Tinker. 1977. *Solute movement in the soil-root system*. Univ. California Press, Berkeley.
19. Oades, J. M. 1978. Mucilages at the root surface. *J. Soil Sci.* 29:1-16.
20. Owusu-Bennoah, E., and A. Wild. 1979. Autoradiography of the depletion zone of phosphate around onion roots in the presence of vesicular-arbuscular mycorrhiza. *New Phytol.* 82:133-140.
21. Rovira, A. P., R. C. Foster, and J. K. Martin. 1979. Origin, nature and nomenclature of the organic materials in the rhizosphere. p. 1-4. In J. L. Harley and R. S. Russell (ed.) *The soil root interface*. Academic Press, New York.