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ON THE FREE BOUNDARY PROBLEM FOR THE MICHAELIS-MENTEN ABSORPTION MODEL FOR ROOT GROWTH

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We have studied the plant root surface as an absorption mechanism and plant root growth, and a growth absorption model is proposed, i.e., the free boundary Michaelis-Menten model.

Differences in nutrient availability and transport between the root surface and the rhizosphere were studied through the mechanism of absorption which manifests itself in the limit expression of Michaelis-Menten kinetics for low concentrations. We solved the resultant equations analytically by the quasi-stationary method with two interface boundary conditions and with boundary and initial conditions. The solution is used to compute growth of root radius.

Several examples of concentration distribution curves in soil and root-soil interface as a function of root radius are plotted. The parameters that are varied are root absorption power, flux velocity, transpiration rate, rhizosphere soil-solution concentration, diffusion coefficient, and buffer power.

Many methods exist for studying the mechanism involved in nutrient uptake. One of the most promising methods is the mathematical model, which can be a satisfactory method of modeling the plant-root system by use of the partial differential equation for convective and diffusive flow to a root (Caasen and Barber 1966; Nye and Marriot 1969; Cushmann 1979, 1980, 1982). In general, these models have not considered computing root growth, but rather they have assumed young roots to be growing at exponential rates (Caasen and Barber 1966; Cushmann 1980, 1982).

In the past, various devices and models have been proposed and analyzed with the purpose of interpreting the growing process as a free boundary problem for the heat-diffusion equation (Lame and Clayperon 1831; Stefan 1889; Carslaw and Jaeger 1959; Crank 1975; Tarzia 1988).

In this article we compute the free boundary (the root-soil interface) a priori unknown through the quasi-stationary method (Stefan 1889; Carslaw and Jaeger 1959). We obtain an analytical solution for the nutrient interface concentration and the interface position (the free boundary).

ANALYSIS (THE FREE BOUNDARY MODEL)

Before developing the present model for the nutrient flow to a root, we make several assumptions, which are the following:

The porous medium is homogeneous and isotropic,

Moisture conditions are maintained at a steady state,

Nutrient uptake occurs at the root surface of the absorption zone,

The roots are smooth cylinders,

The rate of uptake can be described by a Michaelis-Menten type equation,

The nutrient transport occurs via convection and diffusion in the radial direction only (the latter takes place in soil-solution phase only),

The rate of influx at infinite concentration (J_m) and the Michaelis Menten constant (K_m) are independent of the velocity of soil water at the root (v_0), and the diffusion coefficient (D) is independent of the flux,

D and the buffer power b ($b = dC/dC_1$ where C is the total diffusible ion and C_1 is the ion concentration in soil solution) are independent of concentration,

The root system parameters are not changed by root age ($k = J_m/K_m$ = constant),

The velocity of water is not affected by nutrient concentration,

Production or depletion of nutrient by microbial or other activity is null,

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All parameters D, b, k are independent of temperature, in the temperature range normally encountered in root growth,

The net uptake of nutrient is totally available for growth, and

Root hairs do not affect nutrient uptake.

With the above assumptions, the partial differential equation for mass and diffusive transport of nutrient to the root (Cushmann 1979, 1980) is given (in cylindrical coordinates) by

$$D\,C_{rr} + \left[D + \frac{v_0 s_0}{b}\right]\frac{C_r}{r} = C_t \qquad (1)$$

where

$C = C_l$ is the ion concentration in soil solution, $C_r = \dfrac{\partial C}{\partial r}$, $C_{rr} = \dfrac{\partial^2 C}{\partial r^2}$,

$C_t = \dfrac{\partial C}{\partial t}$, r = the position coordinate, t = the time, D = the effective diffusion coefficient, v_0 = the velocity of flux solution at the root surface, b = the buffer power, and s_0 = the initial radius.

Taking into account the idea of the model used for the shrinking core problem for noncatalytic gas-solid reactions (Wen 1968; Tarzia and Villa 1990), we propose the following free boundary problem for root growth (an extensive bibliography for moving and free boundary problems for the heat-diffusion equation is given in Tarzia (1988))[4]

$$\begin{array}{ll}
\text{i) } DC_{rr} + D\alpha_0 \dfrac{C_r}{r} = C_t \quad s(t) < r < R, \quad t > 0, & \\
\text{ii) } C(R, 0) = \Phi(r), \qquad s_0 \le r \le R & \\
\text{iii) } C(R, t) = C_\infty > 0, \qquad t > 0, & (2) \\
\text{iv) } DbC_r(s(t), t) + v_0C(s(t), t) = & \\
\qquad \dfrac{kC(s(t), t)}{1 + \dfrac{kC(s(t), t)}{J_m}} - E = aC(s(t), t)\dot{s}(t) & \\
\text{v) } s(0) = s_0, \qquad 0 < s_0 < R &
\end{array}$$

where i) is the Cushmann equation (Cushmann 1979; 1980), ii) and iii) are the initial and boundary conditions, respectively, iv) are the interface conditions representing the mass nutrient balance, and v) is the initial radius. Function s(t) is the interface position (root radius), $\dot{s}(t) = \dfrac{ds(t)}{dt}$ the interface velocity, a is a stoichiometric coefficient, E is a constant efflux, k is the absorption power of root, R is the rhizosphere radius, and $\alpha_0 = 1 + \epsilon$, $\epsilon = \dfrac{v_0 s_0}{Db} > 0$. Φ(r) is the initial concentration profile (given by equation (14) below).

A schematic diagram of free boundary problem is given in Fig. 1.

We notice that conditions (2-iv) transform the initial problem of solving the linear Cushmann equation into a problem which is nonlinear.

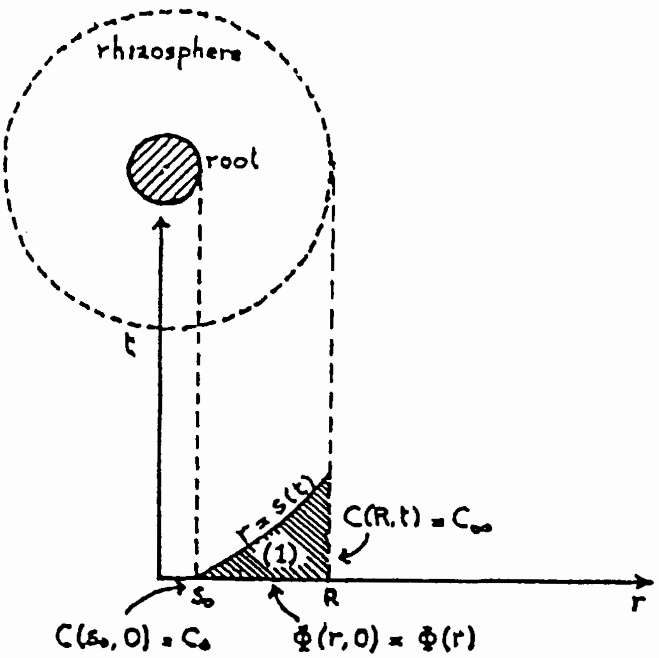
Assuming low concentrations, the uptake nutrient given by Michaelis-Menten expression reduces to

$$\frac{kC(s(t), t)}{1 + \dfrac{kC(s(t), t)}{J_m}} \sim kC(s(t), t) \qquad (3)$$

Thus (2) reduces to the following free boundary problem

$$\begin{array}{ll}
\text{i) } DC_{rr} + D\alpha_0 \dfrac{C_r}{r} = C_t, \quad s(t) < r < R, \quad t > 0, & \\
\text{ii) } C(r, 0) = \Phi(r), \qquad s_0 \le r \le R, & \\
\text{iii) } C(R, t) = C_\infty, \qquad t > 0 & (2\text{-LC}) \\
\text{iv) } DBC_r(s(t), t) + v_0C(s(t), t) = & \\
\qquad kC(s(t), t) - E = aC(s(t), t)\dot{s}(t) & \\
\text{v) } s(0) = s_0, \qquad 0 < s_0 < R. &
\end{array}$$

A method to solve (2-LC) (i.e., compute C = C(r, t), C = C(s(t), t), the free boundary interface r = s(t) a priori unknown) is the quasi-stationary method (Stefan 1889; Carslaw and Jaeger 1959;



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[4] See NOMENCLATURE AND UNITS section at end of this article.

Tarzia 1984). This method assumes that the soil solution concentration is that corresponding to the stationary case in the interval (s(t), R). We thus solve the equation

$$C_{rr} + \alpha_0 \frac{C_r}{r} = 0, \quad s(t) < r < R, \quad t > 0 \qquad (4)$$

with the conditions (2-LC:ii, iii, iv, v) which are called the quasi-stationary method for low concentrations (QSMLC).

The two free boundary conditions (2-LC:iv) can be written by

$$C_r(s(t), t) = g(C(s(t), t)), \qquad t > 0 \qquad (5)$$

$$\dot{s}(t) = f(C(s(t), t)), \qquad t > 0 \qquad (6)$$

where functions g and f are given by

$$g(C) = \frac{1}{Db}\,[(k - v_0)C - E] \qquad (7)$$

$$f(C) = \frac{1}{a}\left[k - \frac{E}{C}\right] \qquad (8)$$

which satisfy the properties

$$f(C) > 0 \Leftrightarrow C > C_p = \frac{E}{k} \qquad (9)$$

$$g(C) > 0 \Leftrightarrow C > C_m = \frac{E}{(k - v_0)}, \qquad (10)$$
$$(C_m > C_p)$$

The solution of the QSMLC problem is given by (see Appendix, Part A)

$$C(r, t) = \beta(t) - \frac{\alpha(t)}{r^{\epsilon}}, \; s(t) < r < R, \qquad (11)$$
$$t > 0$$

where

$$\alpha(t) = \left[\frac{1}{Db}\right]\frac{[(k - v_0)C_\infty - E]}{\dfrac{\epsilon}{s(t)^{1+\epsilon}} + \dfrac{(k - v_0)}{Db}\left[\dfrac{1}{\dot{s}(t)^{\epsilon}} - \dfrac{1}{R^{\epsilon}}\right]} \qquad (12)$$

$$\beta(t) = C_\infty + \frac{\alpha(t)}{R^{\epsilon}} \qquad (13)$$

$$\Phi(r) = C_\infty - \frac{[(k - v_0)C_\infty - E]}{\dfrac{v_0}{s_0{}^{\epsilon}} + (k - v_0)\left[\dfrac{1}{s_0{}^{\epsilon}} - \dfrac{1}{R^{\epsilon}}\right]} \qquad (14)$$
$$\left[\frac{1}{r^{\epsilon}} - \frac{1}{R^{\epsilon}}\right]$$

and s(t) is the unique solution of the following Cauchy problem (see Appendix, Part B)

$$\begin{aligned} \dot{s}(t) &= F(s(t)), \qquad t > 0 \\ s(0) &= s_0 \in (0, R) \end{aligned} \qquad (15)$$

with

$$F(s) = \frac{k}{a}\,[1 - \alpha_3 H(s)] \qquad (16)$$

$$H(s) = \frac{[1 + \alpha_2 G(s)]}{[1 + \alpha_1 G(s)]}, \qquad (17)$$
$$G(s) = s\left[1 - \left(\frac{s}{R}\right)^{\epsilon}\right]$$

$$\alpha_1 = \frac{E}{v_0 s_0 C_\infty} > 0,$$
$$\alpha_2 = \frac{(k - v_0)}{v_0 s_0} > 0, \qquad (18)$$
$$\alpha_3 = \frac{E}{kC_\infty} = \frac{C_p}{C_\infty} > 0$$

Therefore, we obtain, after some elementary manipulations, the interface concentration given by the following expression

$$C(s(t), t) = \frac{C_\infty}{H(s(t))}\; (=C(s(t)), \; t > 0 \qquad (19)$$

that is, the interface concentration does not depend explicitly on variable t.

The solution of the Cauchy problem is computed numerically by the Runge-Kutta method for ordinary differential equations. Figs. 2a, 2b, 2c, 2d, 2e, 2f, and 3a, 3b, 3c, and 3d represent results for the interface concentration C(s(t), t) versus s and the interface position s(t) versus t, respectively, as a function of the dimensionless parameter k/v_0.

From the results of Figs. 2a, 2b, 2c, and 2d we deduce that, if the parameter k/v_0 is small (e.g., 1.5 or 2), accumulation of nutrient is produced in the interface root-soil, there is counterdiffusion, and the root growth is slow. On the other hand, for large values of k/v_0 (e.g., 10), the root growth is fast, and the counterdiffusion is null. The limit value of k/v_0 which produces the counterdiffusion effect depends on the remaining parameters.

From the results of Fig. 2e it follows that if the nutrient concentration C_∞ increases or k/v_0 is large, then the counterdiffusion is null and the growth is faster. On the other hand, as shown

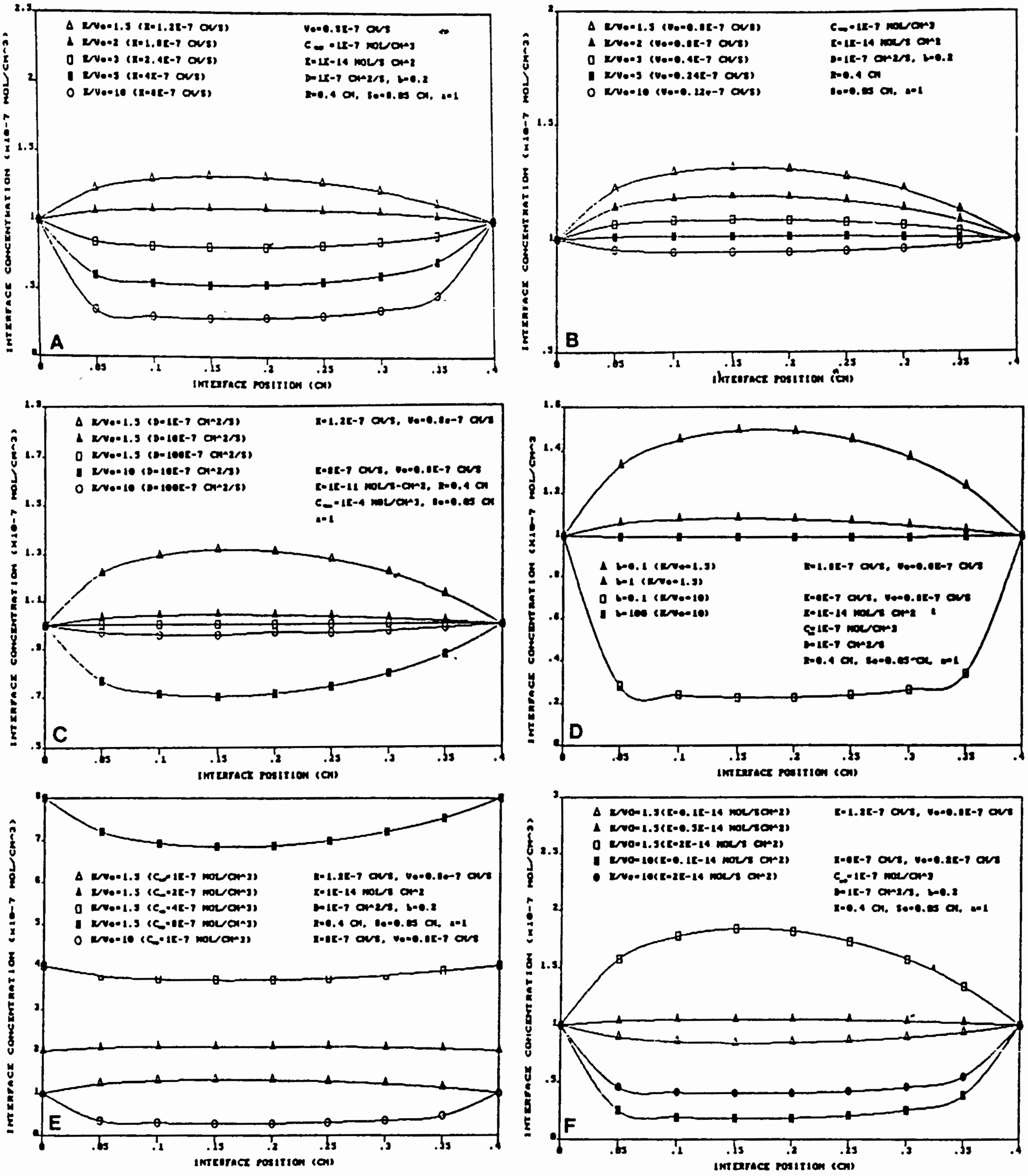

FIG. 2. a) Interface concentration versus root radius as a function of root absorption power. b) Interface concentration versus root radius as a function of flux solution velocity at root surface. c) Interface concentration versus root radius as a function of effective diffusion coefficient. d) Interface concentration versus root radius as a function of buffer power. e) Interface concentration versus root radius as a function of constant rhizosphere soil solution concentration. f) Interface concentration versus root radius as a function of constant efflux.

in Fig. 2f, if E decreases or k/v_0 is large, then the counterdiffusion is null, and the root growth is faster.

Some of the above theoretical results have been observed from an experimental point of view (Barley 1970; Nye and Tinker 1977). Let γ be the parameter defined by

$$\gamma = \frac{E}{(k - v_0)C_\infty} = \frac{\alpha_1}{\alpha_2}$$

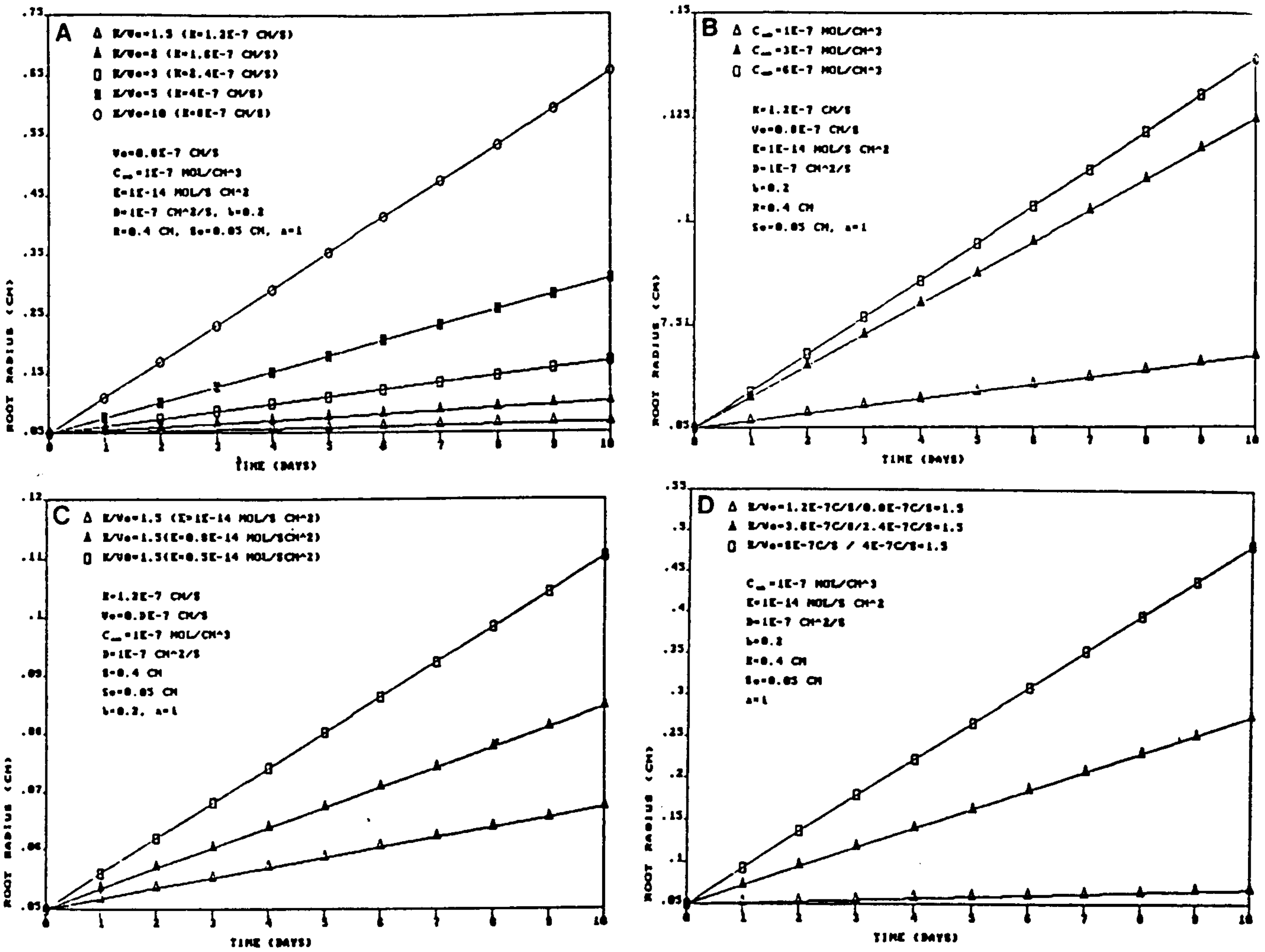

FIG. 3. a) Root radius versus time as a function of root absorption power. b) Root radius versus time as a function of constant rhizosphere soil solution concentration. c) Root radius versus time as a function of constant efflux. d) Root radius versus time as a function of root absorption power and flux solution velocity at root surface.

We can prove that, if (see Appendix, Part C)

$$\text{i)} \quad \gamma = \frac{E}{(k - v_0)C_\infty} < 1$$

implies that C(s(t), t) has a minimum value because the absorption power k is large with respect to v_0 and there is no counterdiffusion.

$$\text{iii)} \quad \gamma = \frac{E}{(k - v_0)C_\infty} = 1$$

implies that C(s(t), t) is constant. (20)

$$\text{iii)} \quad \gamma = \frac{E}{(k - v_0)C_\infty} > 1$$

implies that C(s(t), t) has a maximum value because k is small and the root cannot absorb all the arriving nutrient and there is a counterdiffusion effect.

These results agree with Cushmann's conclusions (Cushmann 1979).

CONCLUSIONS

We conclude from the model presented above that

s = s(t) increases when parameter k or C_∞ increases (Figs. 3a and b).

s = s(t) decreases when parameter E increases (Fig. 3c).

s = s(t) increases when parameter (k/v_0) increases and k and v_0 are large (Fig. 3d).

s = s(t) does not vary in function of the parameters v_0, b, and D because we did not have variations in the corresponding diagrams in a wide range of order of magnitude (1 to 10^5 for each).

$\dot{s} = \dot{s}(t)$ decreases when parameter γ increases, because from (15) through (18) we have for $\dot{s}(t)$ the following representation in function of the parameter γ

$$\dot{s} = \frac{k}{a} \quad 1 - \frac{(k - v_0)}{k} \frac{G(s(t) + \frac{1}{\alpha_2}}{G(s(t) + \frac{1}{\gamma\alpha_2}}, \quad t > 0$$

This conclusion agrees with the first three conclusions.

Finally, we remark that the model presented in this paper gives us a qualitative approach (through a mathematical model) to root growth under the action of only one nutrient with natural limitations in the real situation. Moreover, these conclusions are useful for calibrating numerical models of the more complex nutrient transport and growth problems, or they may be used to isolate the effects of the various parameters in the present model.

APPENDIX

Part A

The general solution of the second order ordinary differential equation (4) is given by

$$C(r) = \beta - \frac{\alpha}{r^{\epsilon}} \tag{A1}$$

where α and β are arbitrary constants.

Because the partial differential equation (4) should be solved in the variable interval $r \in (s(t), R)$, the coefficients α and β must depend on the time t, that is (12) and (13). After some elementary manipulations we deduce that $\alpha(t)$, $\beta(t)$, and $s(t)$ are given by (12), (13), and (15), respectively.

Part B

From (16) we obtain that $F'(s) = \frac{dF}{ds}$

$$\begin{aligned} F'(s) &= -\frac{k\alpha_3}{a} H'(s) \\ &= -\frac{k\alpha_3}{a} (\alpha_2 - \alpha_1) \frac{G'(s)}{[1 + \alpha_1 G(s)]^2} \end{aligned} \tag{B1}$$

that is

$$|F'(s)| \leq \frac{k\alpha_3}{a} |\alpha_2 - \alpha_1| \operatorname{Max}(1, \epsilon) \tag{B2}$$

because

$$\begin{aligned} G'(s) &= 1 - (1 + \epsilon)\left[\frac{s}{R}\right]^{\epsilon}, \\ G'(0) &= 1, \qquad G'(R) = -\epsilon \\ G''(s) &= -\frac{(1 + \epsilon)}{R^{\epsilon}} \epsilon s^{\epsilon - 1} < 0, \\ |G'(s)| &\leq \operatorname{Max}(1, \epsilon) \end{aligned} \tag{B3}$$

From (B2), F′ is a bounded function and therefore the Cauchy problem (15) has a unique solution.

Part C

From (17) and (19) $\left[C(s) = \frac{C_\infty}{H(s)}\right]$ we obtain that (Case $\alpha_1 \neq \alpha_2$)

$$\begin{aligned} C'(s) &= -\frac{C_\infty H'(s)}{[H(s)]^2} \\ &= -\frac{C_\infty(\alpha_2 - \alpha_1)G'(s)}{[1 + \alpha_1 G(s)]^2[H(s)]^2} \end{aligned} \tag{C1}$$

and

$$\begin{aligned} &C'(s) = 0 \Leftrightarrow G'(s) = \\ &0 \Leftrightarrow s = R_0 = \frac{R}{[1 + \epsilon]^{1/\epsilon}} \end{aligned} \tag{C2}$$

From (C2) we notice that the interface concentration has an extreme value at $s = R_0$.

After some elementary manipulations we obtain

$$\begin{aligned} C''(R_0) &= \frac{C_\infty(\alpha_2 - \alpha_1)\epsilon[1 + \epsilon]^{1/\epsilon}}{R[(1 + \alpha_1 G(R_0))H(R_0)]^2} \\ &= d\alpha_2 \left[1 - \frac{E}{(k - v_0)C_\infty}\right] \\ &= d\alpha_2(1 - \gamma), \end{aligned} \tag{C3}$$

where

$$d = \frac{C_\infty \epsilon [1 + \epsilon]^{1/\epsilon}}{R[(1 + \alpha_1 G(R_0))H(R_0)]^2} > 0 \tag{C4}$$

and then we conclude (20).

NOMENCLATURE AND UNITS

r:	Position (radius) coordinate	$[\mathrm{cm}]$
t	Time	$[\mathrm{sec}]$
J_m:	Rate of influx at infinite concentration	$\left[\frac{\mathrm{mol}}{\mathrm{sec\text{-}cm}^2}\right]$
K_m:	Michaelis Menten constant	$\left[\frac{\mathrm{mol}}{\mathrm{cm}^3}\right]$
k:	Absorption power of root	$\left[\frac{\mathrm{cm}}{\mathrm{sec}}\right]$
v_0:	Velocity of flux solution at the root surface	$\left[\frac{\mathrm{cm}}{\mathrm{sec}}\right]$
D:	Effective diffusion coefficient	$\left[\frac{\mathrm{cm}^2}{\mathrm{sec}}\right]$
C:	Total diffusable ion concentration	$\left[\frac{\mathrm{mol}}{\mathrm{cm}^3}\right]$
C_l:	Soil solution concentration	$\left[\frac{\mathrm{mol}}{\mathrm{cm}^3}\right]$
$C(s(t), t)$:	Soil solution concentration at root-soil interface	$\left[\frac{\mathrm{mol}}{\mathrm{cm}^3}\right]$
$\Phi(r)$:	Initial concentration profile	$\left[\frac{\mathrm{mol}}{\mathrm{cm}^3}\right]$
C_∞:	Constant rhizosphere soil solution concentration	$\left[\frac{\mathrm{mol}}{\mathrm{cm}^3}\right]$
s_0:	Initial radius	$[\mathrm{cm}]$
E:	Constant efflux	$\left[\frac{\mathrm{mol}}{\mathrm{sec\text{-}cm}^2}\right]$
$s(t)$:	Instantaneous radius of root	$[\mathrm{cm}]$
$\dot{s}(t)$:	Instantaneous velocity of root-soil interface	$\left[\frac{\mathrm{cm}}{\mathrm{sec}}\right]$
R:	Rhizosphere radius	$[\mathrm{cm}]$
b:	Buffer power	Dimensionless
a:	Stoichiometric coefficient	Dimensionless
α_1, α_2		$\left[\frac{1}{\mathrm{cm}}\right]$
$\alpha_0, \epsilon, \alpha_3, \gamma$		Dimensionless

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