0038-075X/91/1522-0063$03.00/0
SOIL SCIENCE
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August 1991
Vol. 152, No. 2
Printed in U.S.A.

ON THE FREE BOUNDARY PROBLEM FOR THE MICHAELIS-MENTEN ABSORPTION MODEL FOR ROOT GROWTH. II. HIGH CONCENTRATIONS

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Root growth is studied, and a growth absorption model for high concentrations is proposed, i.e., the free boundary Michaelis-Menten model. Nutrient availability and transport between the root surface and the rhizosphere are studied through the Michaelis-Menten type absorption for high concentrations. The resultant equations of the present free boundary problem are used to compute the growth of root radius. Graphics of interface concentrations versus interface position and interface root-soil position versus time are shown as a function of parameters such as the flux velocity, constant efflux, rhizosphere soil solution concentration, diffusion coefficient, and buffer power.

In the literature there exists a great variety of methods for modeling the plant-root system. One of these methods is the one that makes use of the theory of the partial differential equation for convective and diffusive flow to a root. In general, these models have not computed root growth analytically (Classen and Barber 1966, Nye and Marriot 1969, and Cushman 1980, 1982), but we have considered the mathematical problem of free boundary for root growth for low concentrations (Reginato, Tarzia, and Cantero 1990) in a recent paper, to which the present paper is a second part of the model for root growth for high concentrations that we propose; we compute the root-soil interface position and the interface concentration through the quasi-stationary method (Lame and Clayperon 1831, Stefan 1889, Carslaw and Jaeger 1959, and Crank 1984).

ANALYSIS

In the present high concentrations (not saline conditions) model we make analogous assumptions to the model for low concentrations (Reginato, Tarzia, and Cantero 1990), i.e:

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_o), and the diffusion coefficient (D) is independent of the flux, D and the buffer power b ($b = \mathrm{d}C/\mathrm{d}C_1$ 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 (the absorption power $k = J_m/K_m = \text{constant}$),

The velocity of water is not affected by nutrient concentration,

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

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 root growth, and root hairs do not affect the uptake nutrient.

With the above assumptions, the partial differential equation for mass and diffusive transport of nutrient to the root (Cushman 1980, 1892) is given (in cylindrical coordinates) by:

$$DC_{1_{rr}} + \left[D + \frac{v_o s_o}{b}\right]\frac{C_{1_r}}{r} = C_{1_t} \qquad (1)$$

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Received June 12, 1990; accepted Nov. 16, 1990.

where

C_1 is the ion concentration in soil solution, $C_{1r} = \partial C_1/\partial r$,$C_1 1_{rr} = \partial^2 C_1/\partial r^2$, $C_{1t} = \partial C_1/\partial t$, r is the position coordinate, t the time, and s_o the initial radius.

Using an analogous method to that used for root growth for low concentrations (Reginato, Tarzia, and Cantero 1990), we propose the following free boundary problem for root growth:

$$\begin{aligned}
&\text{i) } DC_{1_{rr}} + D\alpha_o C_{1_r}/r = C_{1_t}, \\
&\qquad s(t) < r < R,\ 0 < t \le T, \\
&\text{ii) } C_1(r, 0) = \Phi(r), \\
&\qquad s_o \le r \le R, \\
&\text{iii) } C_1(R, t) = C_\infty > 0, \\
&\qquad 0 < t \le T, \qquad\qquad (2) \\
&\text{iv) } DbC_{1_r}(s(t), t) + \upsilon_o C_1(s(t), t) \\
&\qquad = J_m - E = a\, C_1(s(t), \dot{s}(t), \\
&\text{v)} s(0) = s_o, \\
&\qquad 0 < s_o < R,
\end{aligned}$$

where i) is the Cushman equation; ii) is the initial concentration profile; iii) is the boundary condition on the rhizosphere radius R; iv) are the interface conditions representing the mass nutrient balance with the assumption of high concentration for the uptake nutrient given by Michaelis-Menten expression (3), $kC_1(s(t), t)/1 + kC_1(s(t), t)/J_m \sim J_m$, and υ) is the initial condition for the free boundary $s(t)$ or root radius, a is a stoichiometric coefficient, $E > 0$ is a constant efflux, and $\alpha_o = 1 + \epsilon$, with $\epsilon = \upsilon_o s_o/Db > 0$. $\Phi(r)$ is the initial concentration profile (given by Eq. (14) below).

A method to solve Eq. (2) (that is, to compute $C_1 = C_1(r, t)$, $C_1 = C_1(s(t), t)$, the free boundary interface $r = s(t)$ a priori unknown, and the time T for which a solution exists, i.e., the time for which the influx is null) is the quasi-stationary method (Lame and Clayperon 1831, Stefan 1889, Carslaw and Jaeger 1959, and Crank 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:

$$C_{1_{rr}} + \alpha_o \frac{C_{1_r}}{r} = 0,$$

$$s(t) < r < R,\ 0 < t \le T, \tag{4}$$

with the conditions (2-ii, iii, iv, v), which are called the quasi-stationary method for high concentrations (QSMHC).

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

$$C_{1_r}(s(t),t) = g(C_1(s(t), t),\quad 0 < t \le T, \tag{5}$$

$$\dot{s}(t) = f(C_1(s(t), t),\quad 0 < t \le T, \tag{6}$$

where functions g and f are given by:

$$g(C_1) = \frac{J_m - E - \upsilon_o C_1}{Db} \tag{7}$$

and

$$f(C_1) = \frac{J_m - E}{aC_1} \tag{8}$$

which satisfy the following properties:

$$g(C_1) > 0 \Leftrightarrow 0 < C_1 < C_{1_M} = \frac{J_m - E}{\upsilon_o}, \tag{9}$$

$$f(C_1) > 0,\ \forall\ C_1 > 0, \tag{10}$$

and υ_o satisfies the following inequality:

$$\upsilon_o < \upsilon_{\text{crit}} = \frac{J_m - E}{C_\infty},$$

where υ_{crit} represents the higher velocity below which we have a positive function g.

The solution of the QSMHC problem is given by (see Appendix A):

$$C_1(r, t) = \beta(t) = \frac{\alpha(t)}{r^{\epsilon}},\quad s(t) < r < R,\ 0 < t \le T, \tag{11}$$

where

$$\alpha(t) = \frac{R^{\epsilon};[J_m - E/\upsilon_o - C_\infty]}{1 - [(R/s(t)^{\epsilon}(1 - s_o/s(t))]}, \tag{12}$$

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

$$\Phi(r) = C_\infty + \left[\frac{J_m - E}{v_o} - C_\infty\right]\left[1 - \left(\frac{R}{r}\right)^{\epsilon}\right], \tag{14}$$

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

$$\dot{s}(t) = F(s(t)),\quad 0 < t \le T, \tag{15}$$

$$s(0) = s_o \in (0, R), \tag{16}$$

with

$$F(s) = \left[\frac{J_m - E}{a}\right]\frac{1}{C_1(s)},$$

where

$$C_1(s) = C_\infty + \left[\frac{J_m - E}{1 - \left[\left(\frac{R}{s}\right)^\epsilon \left(1 - \frac{s_o}{s}\right)\right]}\right] \cdot \left[1 - \left(\frac{R}{s}\right)^\epsilon\right], \; 0 < t \leq T. \tag{17}$$

After some elementary manipulations, we find that the interface concentration is given by the following expression:

$$C_1(s(t), t) = C_1(s(t)), \tag{18}$$

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

Moreover, it can be demonstrated that (see Appendix C):

Case A. With the hypothesis $s_o \leq s_\epsilon$ and $K_2 = J_m - E/v_o - C_\infty > 0$:

$$\dot{s}(t) > 0 \Leftrightarrow C_1(s) > 0 \; \forall \; s$$

$$\Leftrightarrow C_\infty - K_2 \, \epsilon \frac{1}{s_o/R \; (1 + \epsilon)^{(1+\epsilon/\epsilon)} - \epsilon} > 0,$$

where

$$s_\epsilon = \frac{R}{\xi_\epsilon} = \frac{R}{(1 + \epsilon)^{1/\epsilon}};$$

Case B. With the hypothesis $s_o > s_\epsilon$ and $K_2 > 0$:

$$C_1(s) > 0 \; \forall \; s \in (s_o, R) \Leftrightarrow$$

$$C_\infty - K_2\left[\left(\frac{R}{s_o}\right)^\epsilon - 1\right] > 0; \quad \text{and}$$

Case C. With the hypothesis $K_2 < 0$:

$$C_1(s) \geqslant C_\infty > 0, \; \forall \; s.$$

By analogy, we arrive at similar propositions for low concentrations (Reginato, Tarzia, and Cantero 1990). These are given by (see Appendix D):

$$\frac{1}{\alpha_3} \geq \frac{1 + \alpha_2 R}{1 + \alpha_1 R} \Rightarrow \dot{s}(t) > 0.$$

The solution of the Cauchy problem (Ince 1956, and Kreider, Kuller, and Ostberg 1968) is computed numerically by the Runge-Kutta method for ordinary differential equations (Conte and Boor 1972). Figures 1a, 1b, 1c, 1d, 1e, 1f, 2a, 2b, and 2c represent the theoretical results for the interface concentration $C_1(s)$ versus the root radius s and the root radius $s(t)$ versus the time t, respectively. The values of parameters used are given for each of them.

From the results of Figs. 1a, 1d, 1e, and 1f, we deduce that for all values of parameters v_o, J_m, D, and b, no counterdiffusion is produced in the interface root-soil in a wide range of order of magnitude (1 to 10^5 for each). From Fig. 1b we deduce that the counterdiffusion is meaningless as a function of the parameter C_∞. On the other hand, from Fig. 1c for large values of E, there exists counterdiffusion, and root growth is low.

From Figs. 2a, 2b, and 2c it follows that if the nutrient concentration C_∞, the diffusion coefficient D, or the constant efflux E increases, then growth is lower, owing to the fact that the effect of these parameters is to increase the soil solution concentration at root-soil interface $s(t)$ and, as a consequence, that the interface velocity $\dot{s}(t)$ is proportional to $1/C_1(s(t))$ growth decreases. Root growth does not vary significantly as a function of the remaining parameters. From the comparison between the present model for root growth for high concentrations and the corresponding model for low concentrations (Reginato, Tarzia, and Cantero 1990), we find that the absorption for low concentrations is more efficient than the mechanism for high concentrations owing to the range of values for $C_1(s)$ and $s(t)$ in each case. This result is valid in the concentration range for the highly specific mechanisms *I* (Epstein, Rains, and Elzam and Epstein 1963 1972), although total growth can be higher when both mechanisms I and II (not specific) operate in parallel (Welch and Epstein 1968, 1969).

CONCLUSIONS

In the present model no limit conditions for root growth in opposition to the case for low concentrations exists. For low concentrations there exists a minimum concentration above which the growth takes place, i.e., the growth stops when $C_1(s) = E/k$; instead, for high concentrations the interface velocity $\dot{s}(t)$ is positive for all value of $C_1(s)$.

One important difference is that there exists counterdiffusion for E and C_∞ for high concentrations. Instead, for low concentrations counterdiffusion is possible for all parameters.

We can remark that the model presented gives us a qualitative approach to root growth under the action of a unique nutrient. This

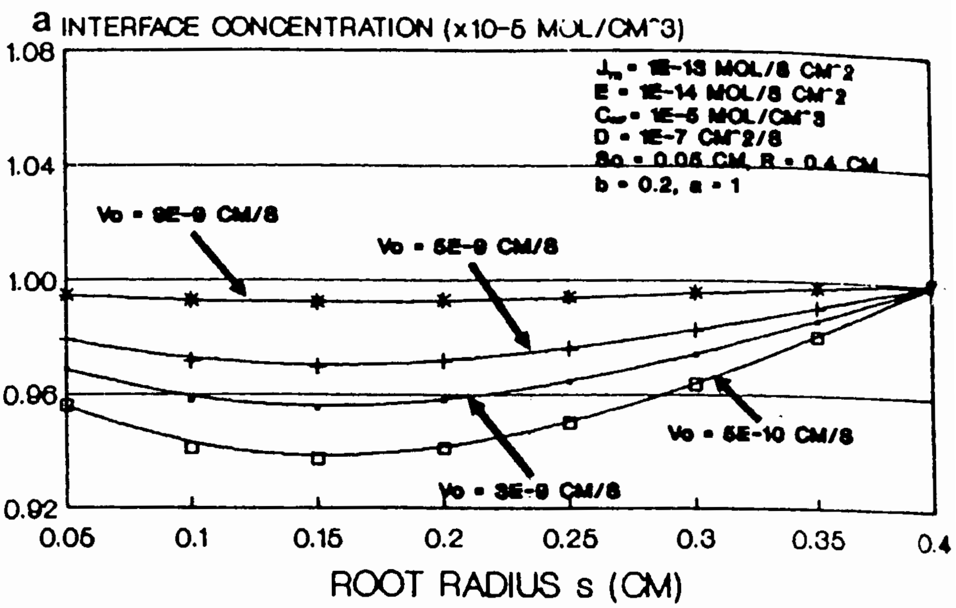

FIG. 1a. Interface concentration $C(s)$ versus the root radius s as a function of flux velocity v_o.

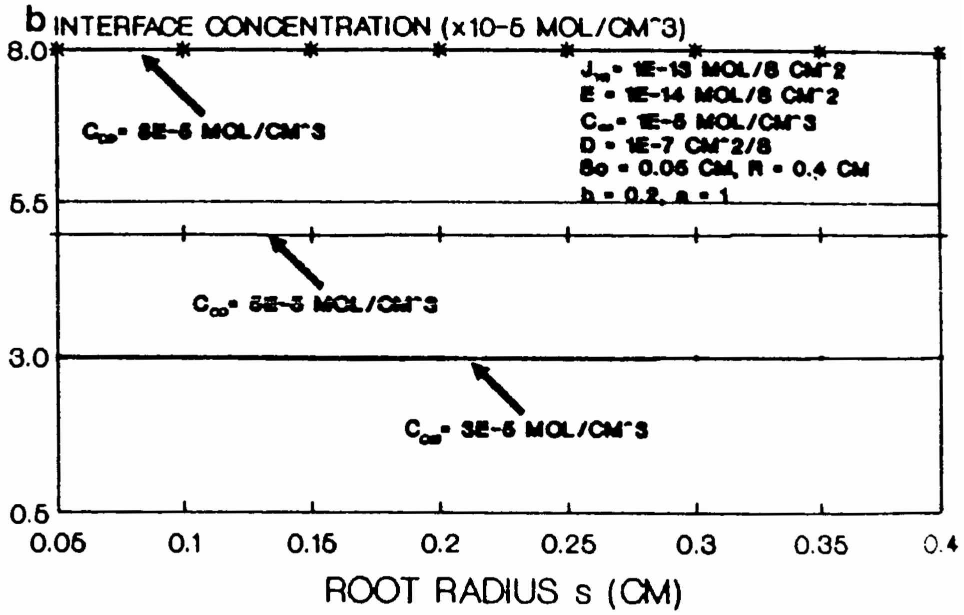

FIG. 1b. Interface concentration $C(s)$ versus root radius s as a function of the rhizosphere solution concentration C_∞.

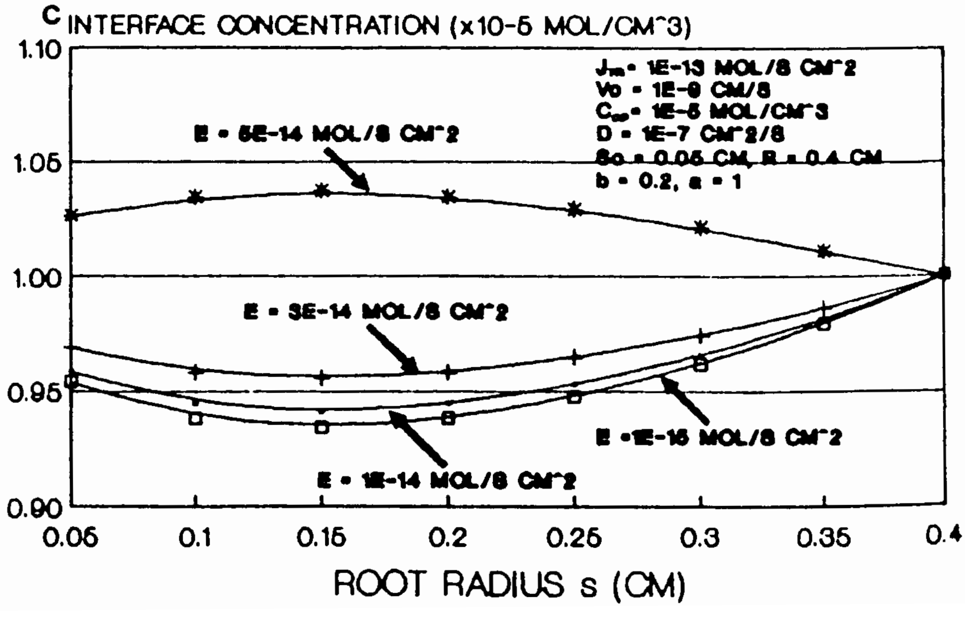

FIG. 1c. Interface concentration $C(s)$ versus root radius s as a function of the efflux E.

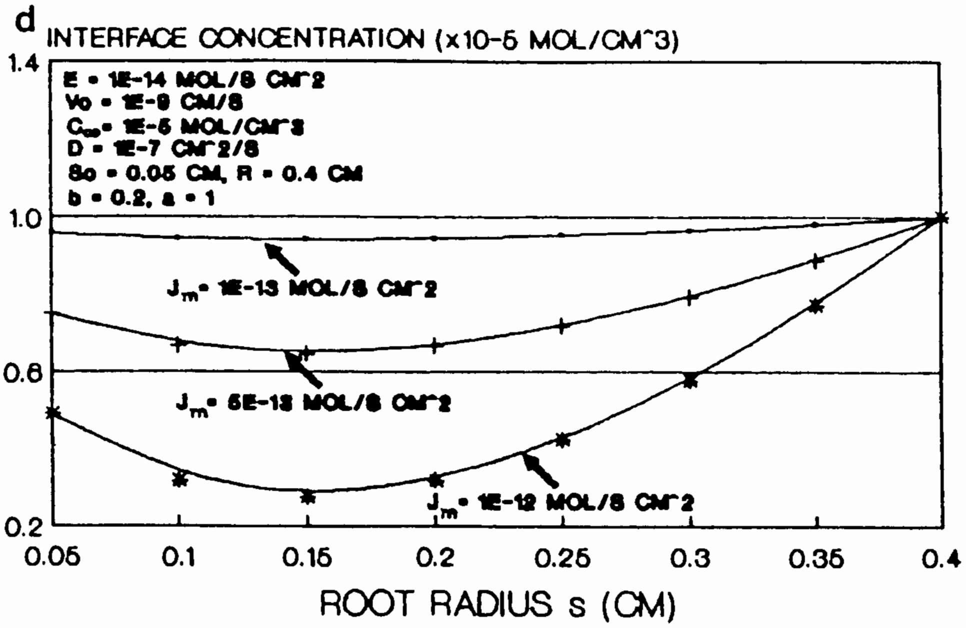

FIG. 1d. Interface concentration $C(s)$ the root radius s as a function of the maximum influx J.

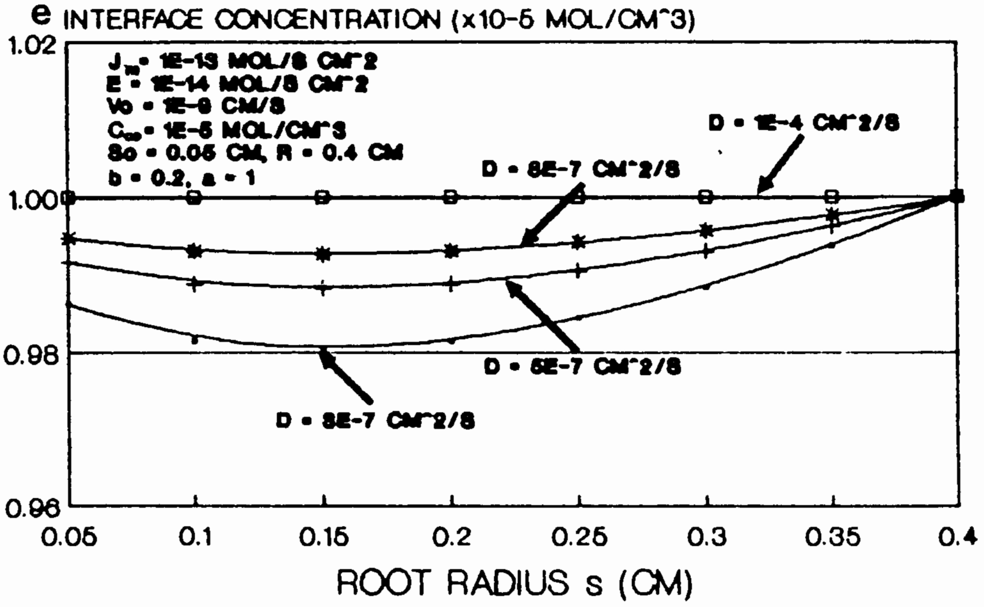

FIG. 1e. Interface concentration $C(s)$ versus root radius s as a function of diffusion coefficient D.

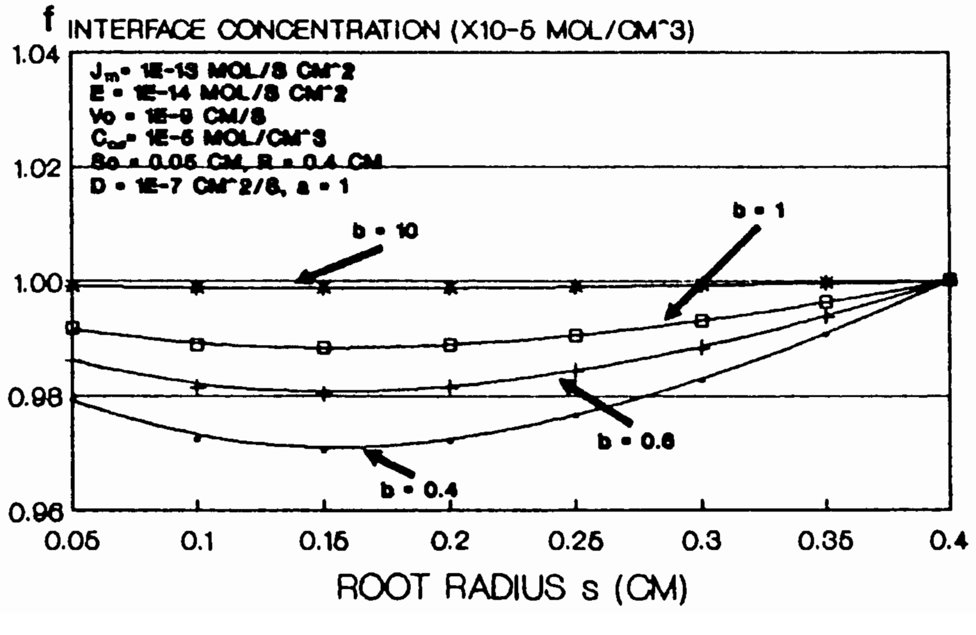

FIG. 1f. Intercase concentration $C(s)$ root radius s as a function of the buffer power b.

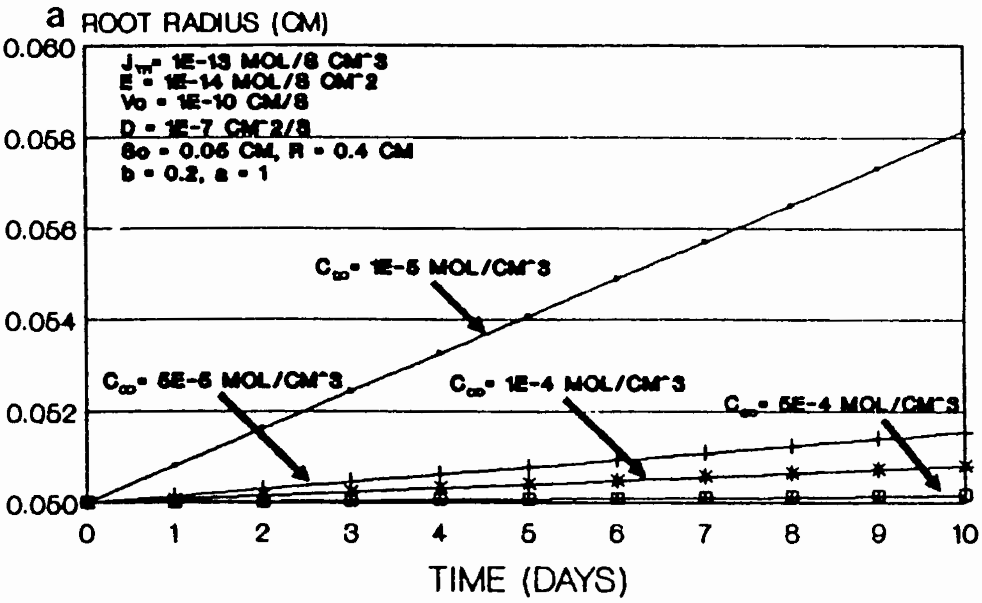

FIG. 2a. Root radius $s(t)$ versus t as a function of rhizosphere soil solution concentration C_∞.

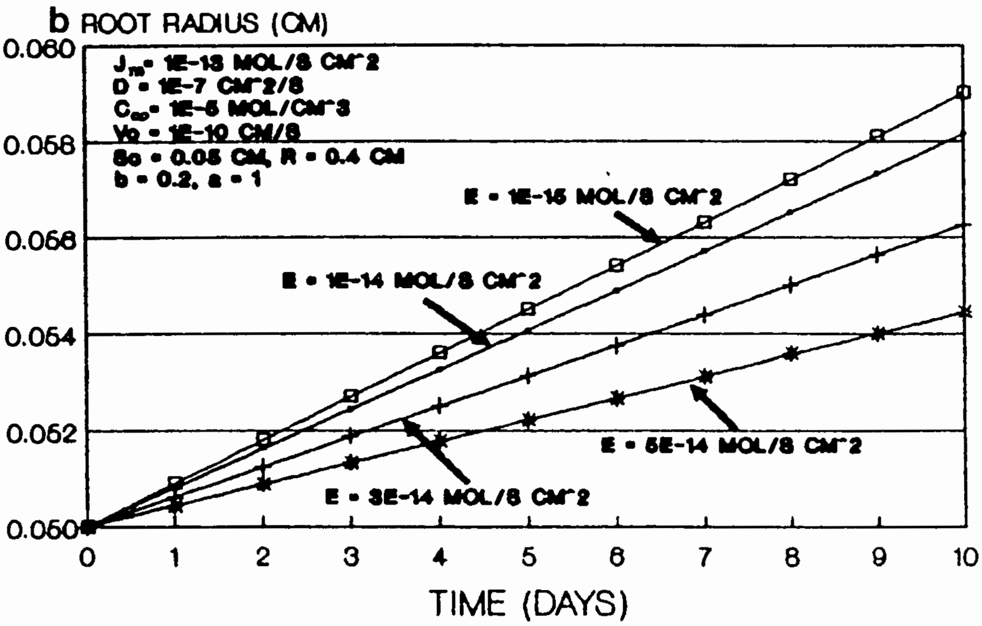

FIG. 2b. Root radius $s(t)$ versus t as a function of efflux E.

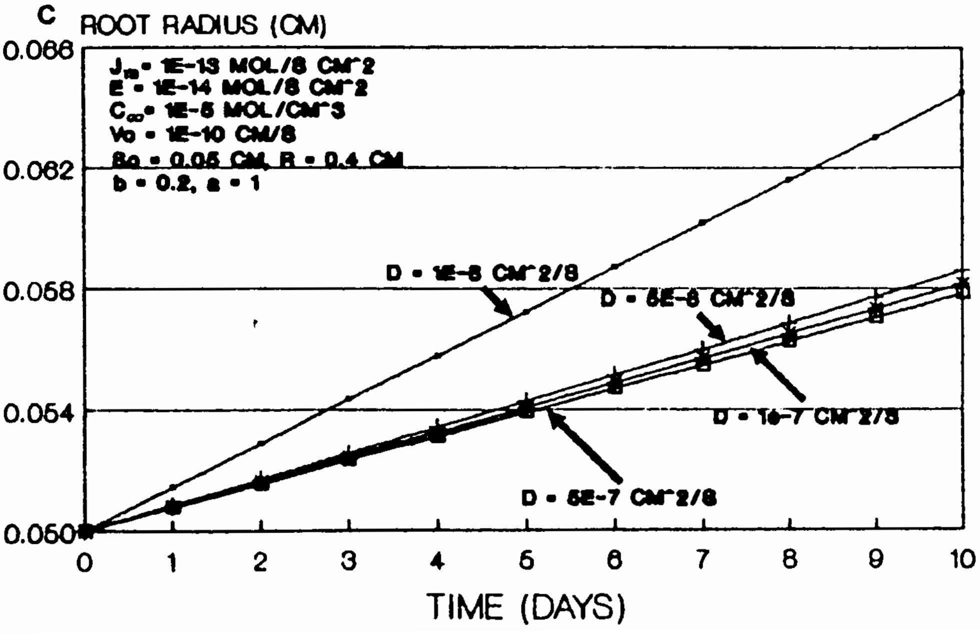

FIG. 2c. Root radius $s(t)$ versus t as a function of diffusion coefficient D.

model is valid for ions that are relatively immobile, e.g., potassium, phosphorus.

Moreover, we assume that both mechanims (low and high concentrations) could be found in a radical system.

Finally, these conclusions may be perfectible, taking into account the dependence of v_o on the nutrient concentration C_∞ and the water content θ. The same conclusions are useful to outline and to understand qualitatively complex nutrient transport and growth problems.

APPENDIX

Part A

The general solution of the second order ordinary differential Eq. (4) is given by:

$$C_1(r) = \beta - \frac{\alpha}{r^{\epsilon}} \tag{A1}$$

where α and β are arbitrary constants.

Because Eq. (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, Eqs. (12) and (13). After some elementary manipulations we deduce that $\alpha(t)$, $\beta(t)$, and $s(t)$ are given by Eqs. (12), (13), and (15), respectively.

Part B

From Eq. (16) we obtain that $(F'(s) = \mathrm{d}F/\mathrm{d}s$, with

$$F(s) = \frac{K_1}{C_1(s)},\ K_1 = \frac{J_m - E}{a} > 0$$

and

$$C_1(s) = C_\infty + \frac{K_2}{1 - W_1(s)}\left[1 - \frac{K_3}{s^{\epsilon}}\right] = C_\infty + K_2 Z(s),$$

$$K_2 = \frac{J_m - E}{v_o} - C_\infty,\ K_3 = R^{\epsilon} > 0,$$

$$W_1(s) = \frac{K_3}{s^{\epsilon}}\left[1 - \frac{s_o}{s}\right] \geq 0,\ s_o \leq s \leq R,$$

$$Z(s) = \frac{1 - K_3/s^{\epsilon}}{1 - W_1(s)},\ s_o < s < R.$$

Therefore, we obtain:

$$F'(s) = K_1\left[-\frac{C_1'(s)}{[C_1(s)]^2}\right] = -\frac{K_1 K_2 Z'(s)}{[C_\infty + K_2(Z(s)]^2}. \tag{B1}$$

Taking $\xi = \dfrac{R}{s}$, we obtain:

$$F'(s) = \frac{K_1 K_2 Y'(\xi)}{[C_\infty + K_2 Y(\xi)]^2}\frac{R}{s^2} = \frac{K_1 K_2}{[C_\infty + K_2 Y(\xi)]^2}\frac{s_o}{s^2} \cdot \frac{\xi^{\epsilon}}{\left[\epsilon^{\epsilon}\left(1 - s_o\xi/R\right) - 1\right]^2} T(\xi), \tag{B2}$$

where $Y(\xi)$ is given by:

$$Y(\xi) = \frac{1 - \xi^{\epsilon}}{1 - \xi^{\epsilon}\left(1 - \dfrac{s_o\xi}{R}\right)},\ 1 < \xi < \frac{R}{s_o},\ \epsilon > 0$$

and verifies the following properties:

$$Y(1^+) = 0^- \quad \text{and} \quad Y(+\infty) = 0^-.$$

Function $T(\xi)$ is given by:

$$T(\xi) = \xi^{\epsilon} - 1 - \epsilon.$$

$T(\xi)$ verifies the following properties:

$$T(1) = -\epsilon < 0,\ T(+\infty) = +\infty,$$

$$T(\xi_o) = T\left(\frac{R}{s_o}\right) = \left(\frac{R}{s_o}\right)^{\epsilon} - 1 - \epsilon$$

$$T'(\xi) = \epsilon\ \xi^{\epsilon - 1} > 0$$

and the equivalance:

$$T(\xi) = 0 \Leftrightarrow \xi^{\epsilon} = 1 + \epsilon$$

$$\Leftrightarrow \xi = (1 + \epsilon)^{1/\epsilon}\left(= \xi_\epsilon = \frac{R}{s_\epsilon}\right). \tag{B3}$$

Therefore, $F'(s)$ is a bounded function.

Part C.

Case A: $s_o \leq s_\epsilon$ and $K_2 > 0$:

$$C_1(s) = C_\infty + K_2 Z(s) \geqslant C_\infty + Z(s_\epsilon) = C_\infty - K_2\epsilon\frac{1}{s_o/R(1 + \epsilon)^{1/1+\epsilon} - \epsilon}. \tag{C1}$$

Case B: $s_o > s_\epsilon$ and $K_2 > 0$:

$$Z(s) \geq Z(s_o) = 1 - \left(\frac{R}{s_o}\right)^{\epsilon} = -\left[\left(\frac{R}{s_o}\right)^{\epsilon} - 1\right],$$

then

$$C_1(s) = C_\infty + K_2 Z(s) \geqslant C_\infty - K_2\left[\left(\frac{R}{s_o}\right) - 1\right]. \quad \text{(C2)}$$

Part D.

Remember that:

$$\dot{s}(t) = \frac{k}{a}\,[1 - \alpha_3 H(s(t))],\ C_1(s) = \frac{C_\infty}{H(s)}$$

where

$$0 < \alpha_1 = \frac{E}{v_o s_o C_\infty} < \alpha_2 = \frac{k - v_o}{v_o s_o}$$

$$\alpha_3 = \frac{E}{k\ C_\infty} < 1$$

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

Defining:

$$H_1(s) = 1 - \alpha_3 H(s). \quad \text{(D1)}$$

The function $H_1(s)$ verifies the following properties:

$$1 > H_1(0^+) = 1 - \alpha_3 > 0$$
$$1 > H_1(R^-) = 1 - \alpha_3 > 0$$

$$H_1'(s) = -\alpha_3 H'(s) \quad \begin{cases} < 0 \Leftrightarrow 0 < s < R_o \\ = 0 \Leftrightarrow s = R_o \\ 0 \Leftrightarrow R_o < s < R \end{cases}$$

and $H(s)$ the equivalence:

$$H'(s) = 0 \Leftrightarrow s = R_o = \frac{R}{(1 + \epsilon)^{1/\epsilon}} < R.$$

Finally, $\dot{s}(t) > 0$ if $H_1(R_o) > 0$, that is:

$$H_1(R_o) > 0 \Leftrightarrow \frac{1}{\alpha_3} > H(R_o) = \frac{1 + \alpha_2\alpha_4}{1 + \alpha_1\alpha_4}, \quad \text{(D2)}$$

where

$$\alpha_4 = \frac{R\ \epsilon}{(1 + \epsilon)^{1+1/\epsilon}}.$$

NOMENCLATURE AND UNITS

r:	Position (radius) coordinate	[cm]
t:	Time	[sec]
J_m:	Rate of influx at infinite concentration	[mol/sec · cm^2]
K_m:	Michaels-Menten constant	[mol/cm^3]
k:	Absorption power of root	[cm/sec]
v_o:	Velocity of flux solution at root surface	[cm/sec]
D:	Effective diffusion coefficient	[cm^2/sec]
C:	Total diffusible ion concentration	[mol/cm^3]
C_1:	Soil solution concentration	[mol/cm^3]
$C_1(s(t), t)$:	Soil solution concentration at root-soil interface	[mol/cm^3]
$\Phi(r)$:	Initial concentration profile	[mol/cm^3]
C_∞:	Constant rhizosphere solution concentration	[mol/cm^3]
s_o:	Initial radius	[cm]
E:	Constant efflux	[mol/sec · cm^2]
$s(t)$:	Instantaneous root radius	[cm]
$\dot{s}(t)$:	Instantaneous velocity of root-soil interface	[cm/sec]
R:	Rhizosphere radius	[cm]
b:	Buffer power	Dimensionless
a:	Stoichiometric coefficient	[1/cm]
α_1, α_2		[1/cm]
α_o, ϵ, α_3, γ		Dimensionless

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