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THE BALANCE INTEGRAL METHOD APPLIED TO ROOT GROWTH OF CROPS

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Abstract—A model for root growth of crops through a free boundary problem is studied.

The resultant effects from differences in nutrient availability and transport between the root surface and the rhizosphere produced by the an active absorption type Michaelis–Menten for low concentrations are studied. The model equations are solved by the mass balance integral method and the numerical solution is used to compute growth of root radius.

Examples of concentration at the root–soil interface curves as a function of root radius and root radius as a function of time are plotted. The parameters which are varied are the root absorption power, flux velocity at the root surface, efflux, rhizosphere soil solution concentration, diffusion coefficient, and buffer power.

INTRODUCTION

One of the methods for studying the nutrient uptake by plant roots, which can be a satisfactory method of modelling the plant–root system is by use of the partial differential equation for convective and diffusive flow to a root [1–4].

In two recent papers [5, 6] a method for computing the root growth through a free boundary problem has been proposed. In these papers, the root soil interface $s(t)$ (the root radius) as a function of time and the interface concentration $C(s)$ as a function of the interface position $s(t)$ are computed by the quasi-stationnary method [7]. The goal of the present paper is to compute the interface position $s(t)$ as a function of t and the interface concentration $C(s(t), t)$ as a function of $s(t)$ and t by application of the mass balance integral method (similar to the heat balance integral method [8, 9]).

PHYSICAL MODEL AND GOVERNING EQUATIONS

Because of the rather complicated scenario of the plant–root system, as a first step toward achieving some understanding of the physical and chemical processes involved, an idealized one-dimensional diffusion–convection model was chosen for this study. It is based on the following assumptions [3, 5, 6]:

- —A vertical cylindrical root summersed in a porous homogeneous and isotropic medium (the soil).
- —Moisture conditions maintained at a steady state.
- —Nutrient uptake occurs at the root surface of the absorption zone.
- —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). Vertical flow in the soil is not considered.
- —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).

- The coefficient diffusion (D) is independent of the flux.
- D and the buffer power b ($b = \mathrm{d}C/\mathrm{d}C_l$, where C is the total diffusable ion concentration and C_l is the ion concentration in soil solution) are independent of concentration.
- The root system parameters are not changed by root age (the root absorption power $k = J_m/K_m = \text{constant}$).
- The convective velocity of water at root surface is not affected by nutrient concentration.
- Production or depletion of nutrient by microbial or other activity is 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 growth.
- Root hairs do not affect the nutrient uptake.
- No vertical flow within the root is considered.

The governing equations for mass and diffuse transport of nutrient to the root [3] as well as the governing equations for root growth in the root–soil interface are given in the following free boundary problem [10–12] (in cylindrical coordinates) by:

$$\text{(i)} \qquad DC_{lrr} + D(1+\epsilon)\frac{C_{lr}}{r} = C_{lt}, \qquad s(t) < r < R, \quad 0 < t < T,$$

$$\text{(ii)} \qquad C_l(r,0) = \Phi(r), \qquad s_0 \le r \le R,$$

$$\text{(iii)} \qquad C_l(R,t) = C_\infty > 0, \qquad 0 < t < T,$$

$$\text{(iv)} \qquad DbC_{lr}(s(t),t) + v_0 C_l(s(t),t) = \frac{kC_l(s(t),t)}{1 + \dfrac{kC_l(s(t),t)}{J_m}} - E, \quad 0 < t < T,$$

$$\text{(v)} \qquad DbC_{lr}(s(t),t) + v_0 C_l(s(t),t) = aC_l(s(t),t)\dot{s}(t), \quad 0 < t < T,$$

$$\text{(vi)} \qquad s(0) = s_0, \quad 0 < s_0 < R, \tag{1}$$

where:

$$C_{lr} = \frac{\partial C_l}{\partial r}, \qquad C_{lrr} = \frac{\partial^2 C_l}{\partial r^2}, \qquad C_{lt} = \frac{\partial C_l}{\partial t},$$

r is the position coordinate, t the time, T is the time for which there exists solution, (i) is the Cushman equation, which is a simple application of the principle of conservation of mass (in soil) under steady moisture conditions with the nutrient flux consisting of two components (diffusive and convective) [3], (ii) and (iii) are the initial and boundary conditions respectively, (iv) and (v) are the interface conditions representing the mass nutrient balance, (iv) expresses the equality of the rate of net mass absorption of the unique ion considered in the active kinetics (right hand side) and the incoming total mass and diffusive flux (left hand side), (v) states the same balance in terms of the free boundary velocity, since a $C_l(s(t),t)\dot{s}(t)$ is again the rate of the mass absorption of the ion [11, 13] and (vi) is the initial condition for the free boundary $s(t)$ (interface root–soil or root radius). $\dot{s}(t) = \mathrm{d}s(t)/\mathrm{d}t$ is the interface velocity, a is a stoichiometric coefficient, E is a constant efflux, R is the rhizosphere radius, C_∞ is the soil solution concentration on the rhizosphere radius, and s_0 is the initial radius. The parameter ϵ is given by

$$\epsilon = \frac{v_0 s_0}{Db} > 0.$$

$\Phi(r)$ is the initial concentration profile (given by the equation (15) below).

From now on, we shall denote C_l by C for convenience in the notation.

The two free boundary conditions (1iv) can be written by:

$$C_r(s(t), t) = g(C(s(t), t)), \quad t > 0 \tag{2}$$

$$\dot{s}(t) = f(C(s(t), t)), \quad t > 0 \tag{3}$$

where functions g and f are given by:

$$g(C) = \frac{1}{Db}\left[\frac{kC}{1 + \frac{k}{J_m}C} - E - v_0 C\right] \tag{4}$$

$$f(C) = \frac{1}{a}\left[\frac{k}{1 + \frac{k}{J_m}C} - \frac{E}{C}\right] \tag{5}$$

which satisfy the following properties:

$$g(C) > 0 \Leftrightarrow C_m^- = \frac{\delta^2(J_m - E) - J_m - d}{2k} < C < C_m^+ = \frac{\delta^2(J_m - E) - J_m + d}{2k} \tag{6}$$

where $d = \sqrt{[\delta^2(J_m - E) - J_m]^2 - 4\delta^2 J_m E}$, with the hypothesis

$$\delta^2 = \frac{k}{v_0} > 1, \qquad \frac{E}{J_m} < \left(1 - \frac{1}{\delta^2}\right)^2,$$

and

$$f(C) > 0 \Leftrightarrow C > C_p = \frac{E}{k\left[1 - \frac{E}{J_m}\right]}, \tag{7}$$

with the hypothesis $E/J_m < 1$.

To solve (1) (that is, to compute $C = C(r, t)$ (in particular, $C = C(s(t), t)$) and the free boundary interface $r = s(t)$ *a priori* unknown) we apply the mass balance integral method [8, 9] to the present case for root growth. The solution is found by integrating the partial differential equation (1i) in r on the domain $(s(t), R)$. Thus:

$$\int_{s(t)}^{R} C_t(r, t)\,\mathrm{d}r = D\int_{s(t)}^{R} C_{rr}(r, t)\,\mathrm{d}r + D(1 + \epsilon)\int_{s(t)}^{R} \frac{C_r(r, t)}{r}\,\mathrm{d}r \tag{8}$$

and we propose:

$$C(r, t) = \Phi(r)[1 + \beta(t)(R - r)] \tag{9}$$

which depends on the parameters of the system and satisfies initial and boundary conditions (1ii) and (1iii), that is:

$$C(r, 0) = \Phi(r) \Leftrightarrow \beta(0) = 0, \tag{10}$$

$$C(R, t) = C_\infty \Leftrightarrow \Phi(R) = C_\infty. \tag{11}$$

We denote $\alpha = \alpha(t)$ by:

$$\alpha(t) = C(s(t), t) \tag{12}$$

which depends on the parameters of the system through $s(t)$, $\Phi(s(t))$ and $\beta(t)$.

Replacing (11) and (12) in equation (8), after some elementary manipulations, the problem (1) reduces to:

$$\begin{aligned} &\int_{s(t)}^{R} C_t(r, t)\,\mathrm{d}r = D[C_r(R, t) - g(\alpha(t))] + D(1 + \epsilon)\left[\frac{C_\infty}{R} - \frac{\alpha(t)}{s(t)} + \int_{s(t)}^{R} \frac{C(r, t)}{r^2}\,\mathrm{d}r\right], \quad t > 0 \\ &\dot{s}(t) = f(\alpha(t)), \quad t > 0, \qquad s(0) = s_0. \end{aligned} \tag{13}$$

Using the approximation $kC/(1+k/J_mC) \approx kC$ (valid for low concentration), and replacing (9) in equation (13), after some elementary manipulations we obtain the following system of two coupled ordinary differential equations (see Appendix) (valid for the cases $\epsilon \neq 1, 2$):

$$\frac{\mathrm{d}\beta(t)}{\mathrm{d}t} = F_1(F_2+F_3+F_4+F_5+F_6+F_7), \qquad \beta(0)=0$$

$$\frac{\mathrm{d}s(t)}{\mathrm{d}t} = \frac{1}{a}\left[k - \frac{E}{\Phi(s(t))[1+\beta(t)(R-s(t))]}\right], \qquad s(0)=s_0 \tag{14}$$

and

$$\Phi(r) = C_\infty + A\left[1-\left(\frac{R}{r}\right)^{\epsilon}\right] \tag{15}$$

where:

$$F_1 = \frac{D}{R\left\{(C_\infty+A)[R-s(t)] + \dfrac{AR^{\epsilon}s^{(1-\epsilon)}(t)-AR}{(1-\epsilon)}\right\} - \left\{\dfrac{C_\infty+A}{2}(R^2-s^2(t)) + \dfrac{AR^{\epsilon}s^{(2-\epsilon)}(t)-AR^2}{(2-\epsilon)}\right\}}, \tag{16}$$

$$F_2 = \frac{A\epsilon}{R} - C_\infty\beta(t) - \frac{1}{Db}[\Phi(s(t))[1+\beta(t)(R-s(t))](k-v_0)-E], \tag{17}$$

$$F_3 = (1+\epsilon)\frac{C_\infty}{R} - (1+\epsilon)\frac{\Phi(s(t))[1+\beta(t)(R-s(t))]}{s(t)}, \tag{18}$$

$$F_4 = (1+\epsilon)(C_\infty+A)(1+\beta(t)R)\left[\frac{1}{s(t)}-\frac{1}{R}\right], \tag{19}$$

$$F_5 = -(1+\epsilon)\beta(t)(C_\infty+A)\ln\left(\frac{R}{s(t)}\right), \tag{20}$$

$$F_6 = \frac{(1+\epsilon)}{\epsilon}A\beta(t)R^{\epsilon}\left[\frac{1}{s^{\epsilon}(t)}-\frac{1}{R^{\epsilon}}\right], \tag{21}$$

$$F_7 = -AR^{\epsilon}[1+\beta(t)R]\left[\frac{1}{s^{\epsilon+1}(t)}-\frac{1}{R^{\epsilon+1}}\right], \tag{22}$$

$$A = \frac{E-(k-v_0)C_\infty}{k\left[1-\left(\dfrac{R}{s_0}\right)^{\epsilon}\right]-v_0}. \tag{23}$$

Remark 1. The initial profile concentration $\Phi(r)$, given by the equation (15) above, has been computed by the quasi-stationary method [4] and it is determinated by the system, similarly to the Cushman's prediction [4].

Remark 2. For the particular cases $\epsilon = 1$ and 2, we can obtain a system similar to (14) of two ordinary differential equations.

Remark 3. For the general rank of concentration C we can obtain a similar system to (14) of two ordinary differential equations.

The solution of system (14) is computed numerically by the Runge–Kutta method for a system of ordinary differential equations. Figures 1–12 represent results for the interface concentration $C(s(t), t)$ vs s and the interface position $s(t)$ vs t respectively as a function of the dimensionless parameter $\delta^2 = k/v_0$.

CONCLUSIONS

We conclude from the model presented above that the free boundary $s = s(t)$ increases when absorption power k increases (Fig. 2) (i.e. the dimensionless parameter k/v_0 increases with

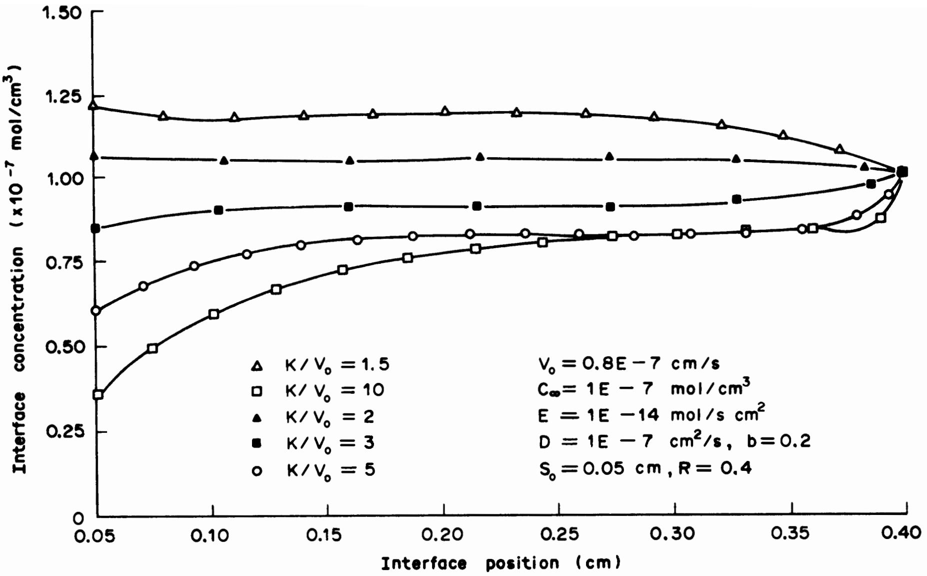

Fig. 1. Interface concentration $C(s)$ vs s as a function of absorption power k.

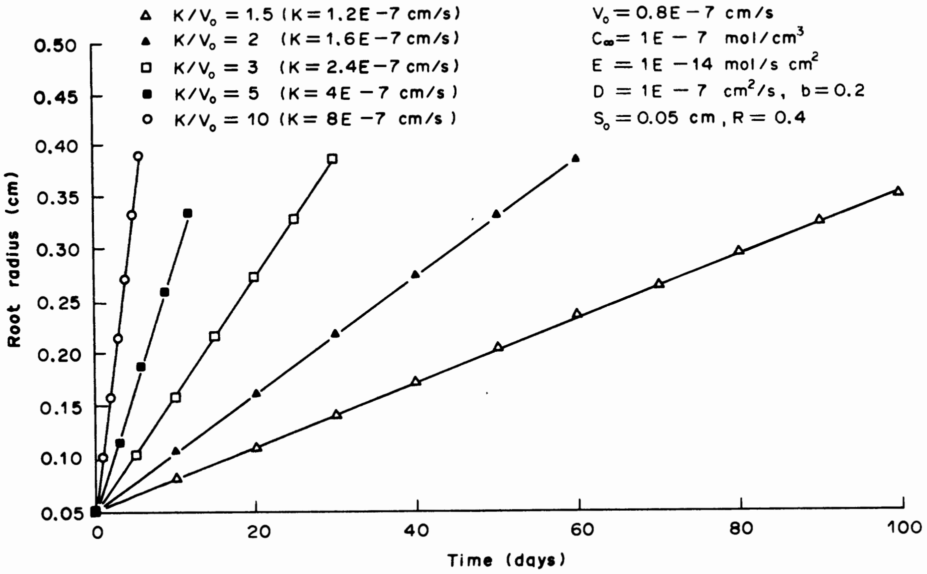

Fig. 2. Root radius $s(t)$ vs t as a function of absorption power k.

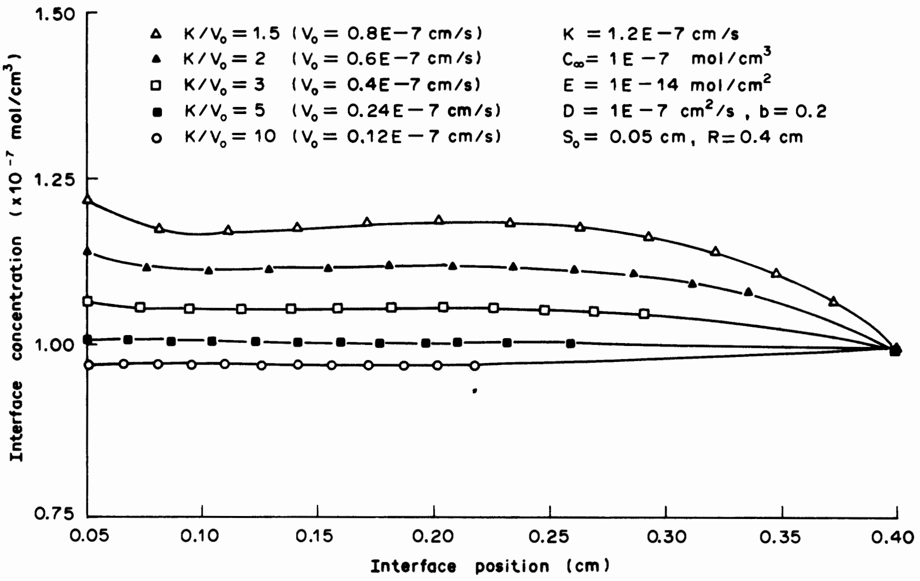

Fig. 3. Interface concentration $C(s)$ vs s as a function of flux velocity at root surface v_0.

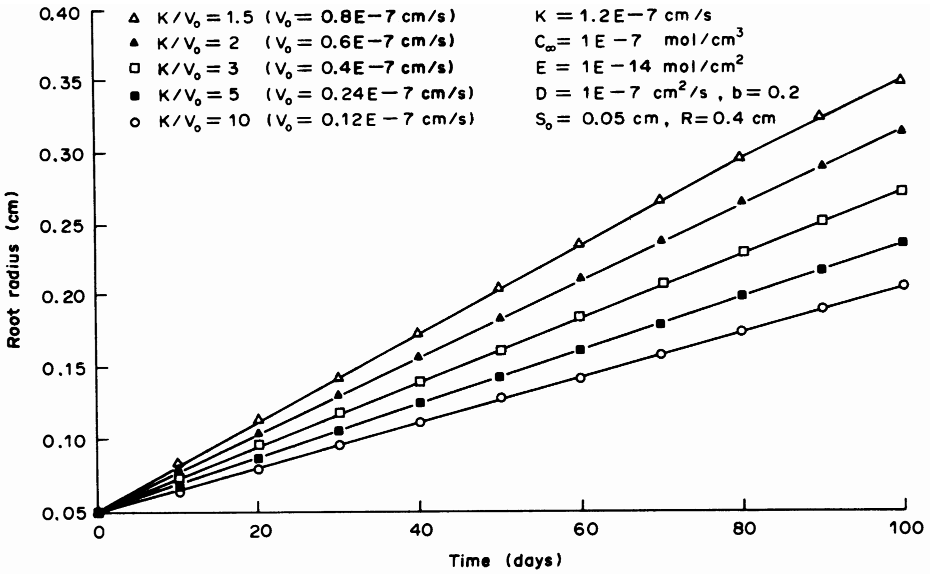

Fig. 4. Root radius $s(t)$ vs t as a function of flux velocity at root surface v_0.

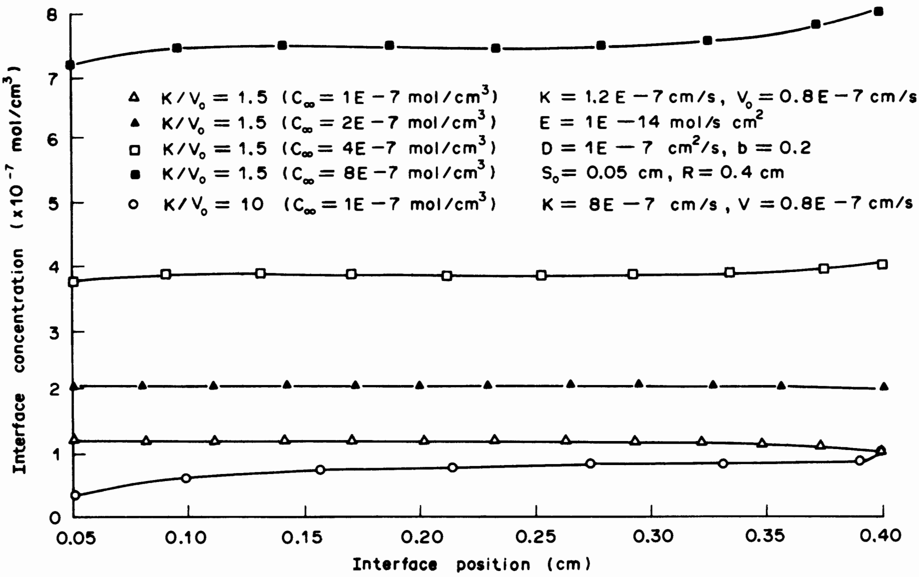

Fig. 5. Interface concentration $C(s)$ vs s as a function of soil solution concentration at rhizosphere C_∞.

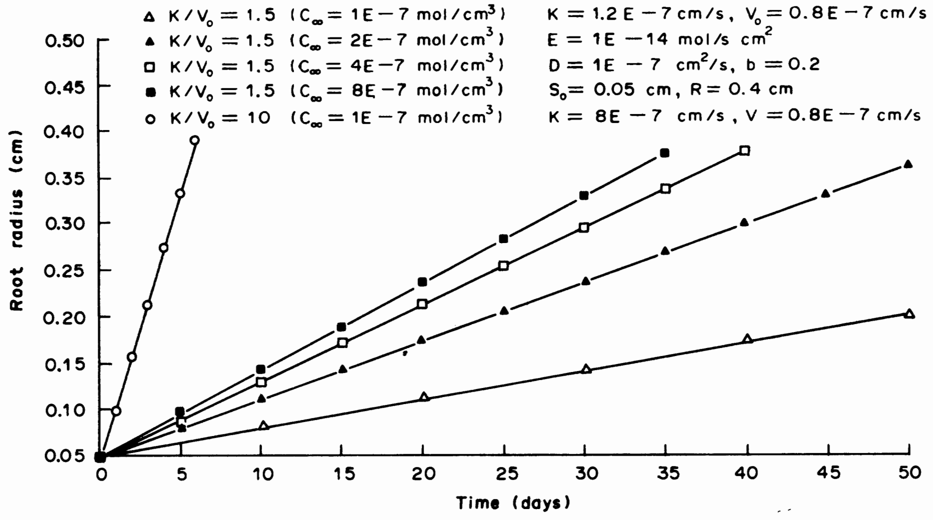

Fig. 6. Root radius $s(t)$ vs t as a function of soil solution concentration at rhizosphere C_∞.

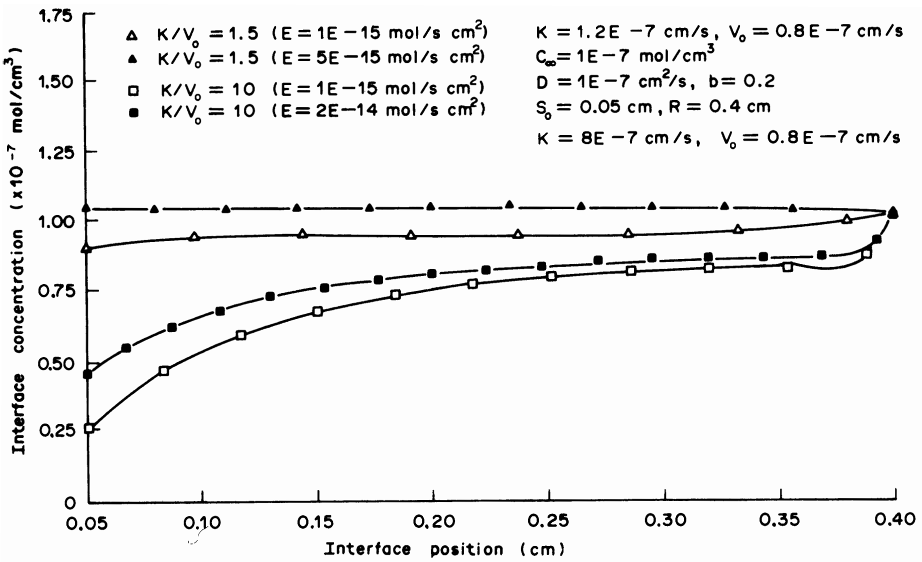

Fig. 7. Interface concentration $C(s)$ vs s as a function of efflux E.

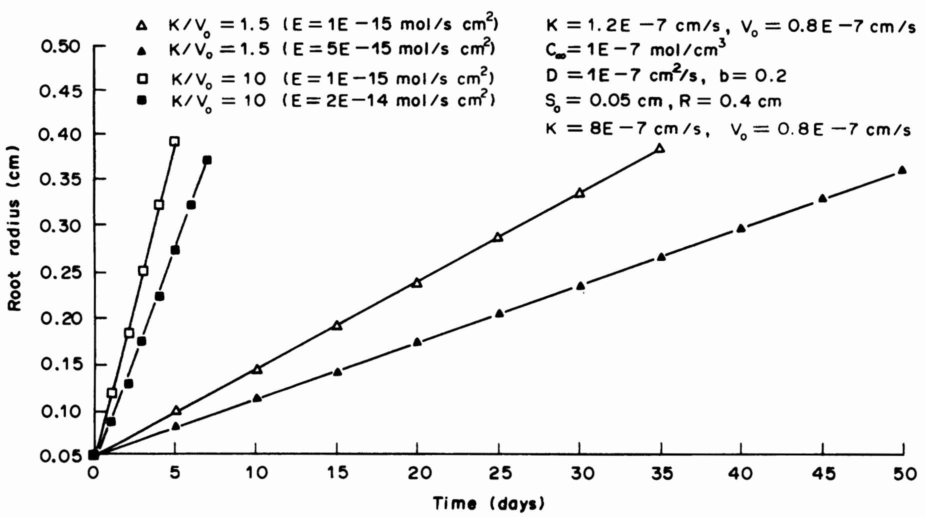

Fig. 8. Root radius $s(t)$ vs t as a function of efflux E.

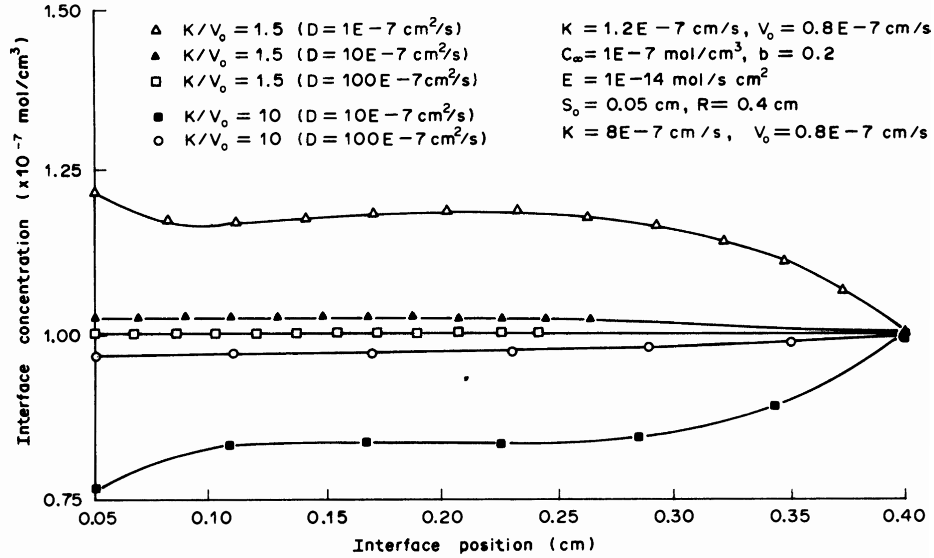

Fig. 9. Interface concentration $C(s)$ vs s as a function of diffusion coefficient D.

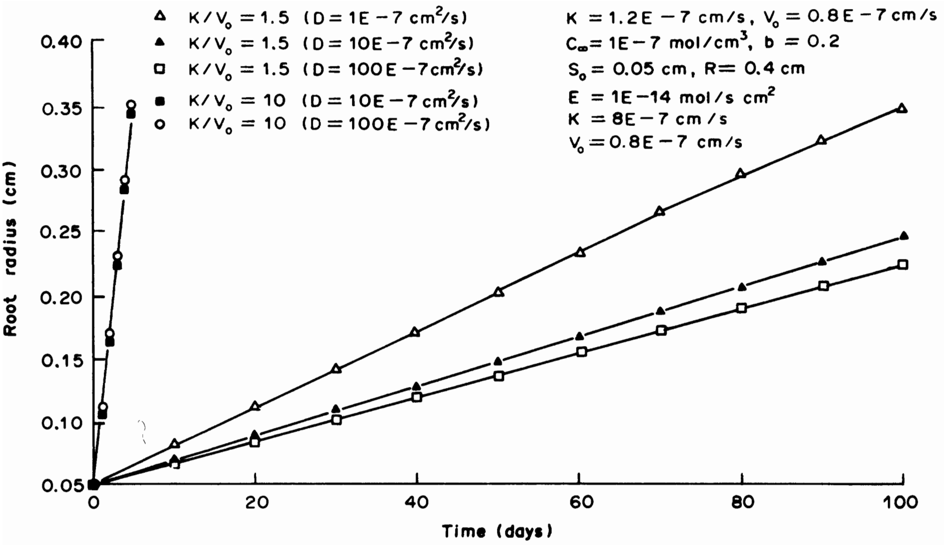

Fig. 10. Root radius $s(t)$ vs t as a function of diffusion coefficient D.

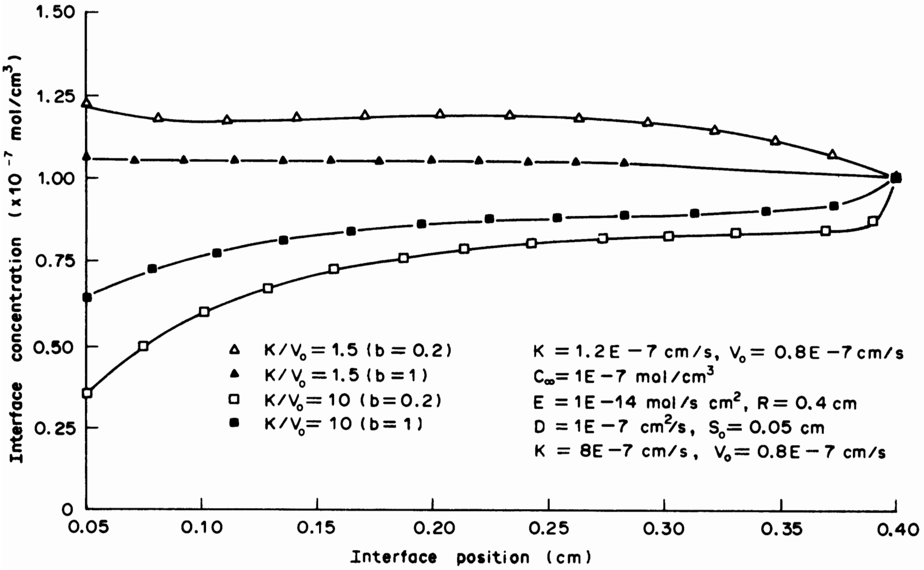

Fig. 11. Interface concentration $C(s)$ vs s as a function of buffer power b.

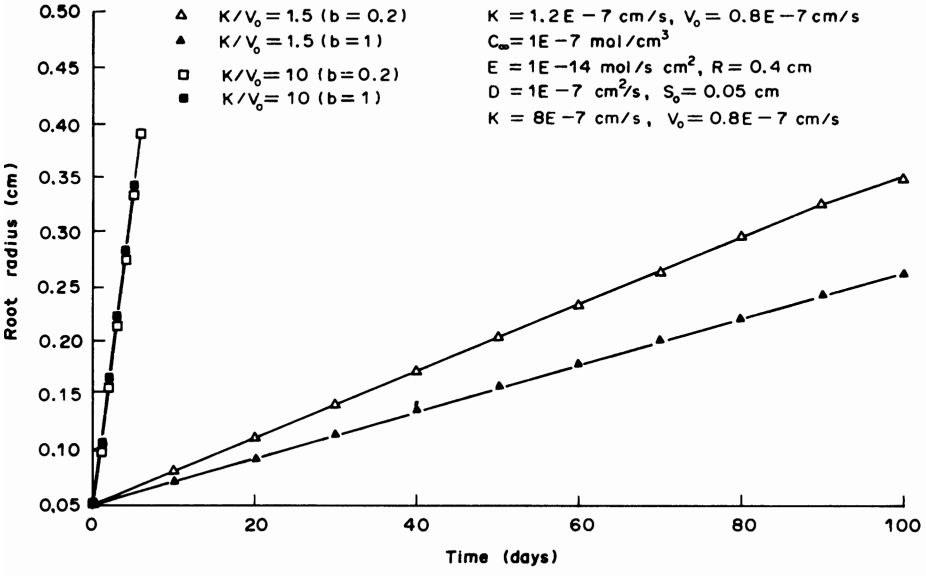

Fig. 12. Root radius $s(t)$ vs t as a function of buffer power b.

$v_0 = \text{const.}$) or when the soil solution concentration C_∞ increases (Fig. 6). Moreover, $s = s(t)$ decreases when the efflux E increases (Fig. 8). Likewise, $s = s(t)$ decreases when the buffer power b (Fig. 12) or the diffusion coefficient D (Fig. 10) increases, although this effect is meaningless for high values (e.g. 10) of the dimensionless parameter k/v_0. Moreover, $s = s(t)$ increases when the flux velocity at the root surface v_0 increases (Fig. 4) (i.e. the parameter k/v_0 decreases with $k = \text{const.}$).

The behavior of interface concentration $C(s(t), t)$ as a function of k, v_0, C_∞, E, D, and b (Figs 1, 3, 5, 7, 9, 11) is quite similar to results obtained by the quasi-stationary method applied to the same model [5]. For example, in Fig. 5, for $\delta^2 = k/v_0 = 1.5$ the interface soil solution concentration increases when the rhizosphere soil solution concentration C_∞ increases. Instead, for $\delta^2 = k/v_0 = 10$ (with $v_0 = \text{const.}$, i.e. k is greater than before) a greater depletion occurs for the interface soil solution concentration which implies a faster growth for the root radius (see Fig. 6).

On the other hand, by comparison of the results obtained in [5] by the quasi-stationary method and in this paper by the balance integral method we can conclude that: first, the qualitative behavior of the results is quite similar for both methods, and secondly the balance integral method give us a more detailed theoretical information, for example the variation of $s(t)$ vs t with respect to the parameter v_0 is negligible for the quasi-stationary method [5] (see Fig. 4).

Thus, we can remark that the present model gives us a qualitative approach to root growth under the absorption of only one nutrient, with natural limitations in the real situation. Moreover, these conclusions are useful to outline more complex models for nutrient transport and root growth.

Finally, we remark that the present formulation is also valid for the any rank of concentrations with appropriate functions g and f.

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APPENDIX

Replacing (9) in equation (13), after some manipulations, we obtain:

$$\int_{s(t)}^{R} C_t(r, t)\,\mathrm{d}r = \int_{s(t)}^{R} \Phi(r)\dot{\beta}(t)(R - r)\,\mathrm{d}r = R\dot{\beta}(t)\int_{s(t)}^{R} \Phi(r)\,\mathrm{d}r - \dot{\beta}(t)\int_{s(t)}^{R} r\Phi(r)\,\mathrm{d}r$$

and, taking into account (15) and (23), we obtain:

$$\int_{s(t)}^{R} \Phi(r)\,\mathrm{d}r = C_\infty \int_{s(t)}^{R} \mathrm{d}r + A\int_{s(t)}^{R} \mathrm{d}r - AR^{\epsilon}\int_{s(t)}^{R} r^{-\epsilon}\,\mathrm{d}r$$

$$= (C_\infty + A)[R - s(t)] - \frac{AR}{(1-\epsilon)} + \frac{AR^{\epsilon}}{(1-\epsilon)} s^{(1-\epsilon)}(t) \quad (\text{with } \epsilon \neq 1),$$

$$\int_{s(t)}^{R} r\Phi(r)\,\mathrm{d}r = C_\infty \int_{s(t)}^{R} r\,\mathrm{d}r + A\int_{s(t)}^{R} r\,\mathrm{d}r - AR^{\epsilon}\int_{s(t)}^{R} r^{(1-\epsilon)}\,\mathrm{d}r$$

$$= \left(\frac{C_\infty + A}{2}\right)[R^2 - s^2(t)] - \frac{AR^2}{(2-\epsilon)} + \frac{AR^{\epsilon}}{(2-\epsilon)} s^{(2-\epsilon)}(t), \quad (\text{with } \epsilon \neq 2),$$

then:

$$\int_{s(t)}^{R} C_t(r,t)\,\mathrm{d}r = R\dot{\beta}(t)\left[(C_\infty + A)[R - s(t)] - \frac{AR}{(1-\epsilon)} + \frac{AR^{\epsilon}}{(1-\epsilon)} s^{(1-\epsilon)}(t)\right]$$

$$- \dot{\beta}(t)\left[\left(\frac{C_\infty + A}{2}\right)[R^2 - s^2(t)] - \frac{AR^2}{(2-\epsilon)} + \frac{AR^{\epsilon}}{(2-\epsilon)} s^{(2-\epsilon)}(t)\right] \tag{A1}$$

Similarly, we obtain:

$$\int_{s(t)}^{R} \frac{C(r,t)}{r^2}\,\mathrm{d}r = \int_{s(t)}^{R} \frac{1}{r^2}\left[C_\infty + A\left[1 - \left(\frac{R}{r}\right)^{\epsilon}\right]\right][1 + \beta(t)(R - r)]\,\mathrm{d}r$$

$$= [(C_\infty + A)[1 + \beta(t)R]]\int_{s(t)}^{R} \frac{\mathrm{d}r}{r^2} - [AR^{\epsilon}[1 + \beta(t)R]]\int_{s(t)}^{R} \frac{\mathrm{d}r}{r^{\epsilon+2}}$$

$$- [\beta(t)(C_\infty + A)]\int_{s(t)}^{R} \frac{\mathrm{d}r}{r} + A\beta(t)R^{\epsilon}\int_{s(t)}^{R} \frac{\mathrm{d}r}{r^{\epsilon+1}}$$

$$= [(C_\infty + A)[1 + \beta(t)R]]\left[\frac{1}{s(t)} - \frac{1}{R}\right] - \frac{[AR^{\epsilon}[1 + \beta(t)R]]}{1+\epsilon}\left[\frac{1}{s^{\epsilon+1}(t)} - \frac{1}{R^{\epsilon+1}}\right]$$

$$- \beta(t)(C_\infty + A)\ln\frac{R}{s(t)} + \frac{A\beta(t)R^{\epsilon}}{\epsilon}\left[\frac{1}{s^{\epsilon}(t)} - \frac{1}{R^{\epsilon}}\right]. \tag{A2}$$

Finally, replacing (A1) and (A2) in equation (13), after elementary manipulations, we obtain the system (14).

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NOMENCLATURE

r	Position (radius) coordinate (cm).
t	Time (s).
J_m	Rate of influx at infinite concentration (mol/s-cm^2).
K_m	Michaelis–Menten constant (mol/cm^3).
k	Absorption power of root (cm/s).
v_0	Velocity of flux solution at root surface (cm/s).
D	Effective diffusion coefficient (cm^2/s).
C	Total diffusable ion concentration (mol/cm^3).
C_l	Soil solution concentration (mol/cm^3).
$C(s(t), t)$	Soil solution concentration at root–soil interface (mol/cm^3).
$\Phi(r)$	Initial concentration profile (mol/cm^3).
C_∞	Constant rhizosphere soil solution concentration (mol/cm^3).
E	Constant efflux (mol/s-cm^2).
R	Rhizosphere radius (cm).
s_0	Initial radius (cm).
$s(t)$	Instantaneous root radius (cm).
$\dot{s}(t)$	Instantaneous velocity of root–soil interface (cm/s).
b	Buffer power (dimensionless).
a	Stoichiometric coefficient (dimensionless).
ϵ	Parameter (dimensionless).