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Analytical study of the effects of some soil and plant parameters on root growth due to absorption of one mobile ion: A free-boundary model

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Abstract

The object of our study is: a model for root growth through a free-boundary problem and the effects resulting from differences in nutrient availability and transport of only one mobile nutrient between the root surface and the rhizosphere produced by an absorption Michaelis-Menten for low and high concentrations. The model equations are solved by two methods: the quasi-stationary method and the balance integral method. The numerical solutions are used to compute radial root growth. Curves of nutrient concentration at the root-soil interface, curve as a function of root radius as well as curves representing 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 radius, diffusion coefficient, buffer power, and maximum influx. The two methods show the theoretical results for radial root growth in the range of low and high concentrations. The balance integral method provides more detailed information.

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. Simulation models for nutrient uptake have frequently been used in the evaluation of the effect of soil and root characteristics on nutrient uptake (Claassen and Barber, 1976; Cushman, 1982; Nye and Marriot, 1969). These models have only considered nutrient uptake and have supposed an exponential root growth, without taking into account effects of coupling between nutrient transport and root growth. Because of the difficulties in modelling these complex processes, in recent articles (Reginato et al., 1990, 1991), as a first approximation to a real, more complete description, a method for computing the effects on root growth owing to absorption of one nearly immobile nutrient by means of a free-boundary problem has been proposed. In these article, the root radius $s(t)$ as a function of time and the interface concentration $C(s)$ as a function of the root radius $s(t)$ are computed by the quasi-stationary method (Crank, 1984) with a contour condition representing a fixed rhizosphere border. Also, the interface concentration $C(s(t), t)$ as an explicit function of $s(t)$, and the time t, as the root radius $s(t)$ vs. t are computed by the balance integral method (Goodman, 1958; Reginato and Tarzia, 1993). Both methods are based on the principle of conservation of mass in the soil as well as at the root-soil interface. The goal of the present paper is to compute the root radius $s(t)$ as a function of t, and the interface concentration $C(s(t), t)$ as a function of $s(t)$ through the quasi-stationary and the balance integral methods with a null flux condition on the rhizosphere border valid for mobile ions, in order to estimate the effects of different parameters on root growth for low and high concentrations (not saline conditions).

The free boundary 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, and idealized one-dimension diffusion-convection ion transport and radial root growth model was chosen for this study. As described in Reginato et al., (1990, 1991) it is assumed that: a vertical cylindrical root is immersed in a porous homogeneous and isotropic medium (the soil) while moisture, temperature, and light conditions are assumed maintained at a steady state. It is assumed that the nutrient uptakes occurs at the root absorption zone, and the root hairs are not considered in the present model. The rate of uptake can be described by a Michaelis Menten equation, and the rate of influx at infinite concentrations (J_m) and the Michaelis Menten constant (K_m) are independent of the flux velocity of soil solution at the root (v_0). The nutrient transport occurs via convection and diffusion in the radial direction only (the latter takes place in the soil solution phase only). It is assumed that the diffusion coefficient (D) and the buffer power (b) are independent of nutrient concentration, which implies that there is a linear relation between C and C_1, where C is the total diffusable ion concentration and C_1 is the ion concentration in the soil solution. No allowance for a change in J_m, K_m, or E (efflux) with age is made. It is also assumed that the coefficient diffusion is independent of the flux, and the convective velocity of water at the root surface is not affected by nutrient concentration. Production or depletion of nutrients by microbial or other activity is considered null, and owing to the proposed model not taking into account the energy balance implicit in the root metabolism, we assumed that the nutrient taken up is totally available for root growth. At this point, only a fraction is available for root growth and the remaining nutrient is available for shoot growth. So, we arrive at only qualitative conclusions. From now on, we shall denote C_1 by C for notational convenience. The governing equations for convective and diffusive transport of nutrients to the root (Cushman, 1982) as well as the governing equations for root growth at the root-soil interface for low concentrations ($J_m \sim kC$) are given in the following free-boundary problem for one phase (the soil) (Crank, 1984; Tarzia, 1988; Tarzia and Villa, 1989). In order to simplify the model, without loss of generality, radial growth in cylindrical coordinates is considered.

$$
\begin{array}{lll}
\text{(i)} & DC_{rr} + D(1+\epsilon)\dfrac{C_r}{r} = 0\,, & s(t) < r < R, \\
 & & 0 < t < T \\
\text{(ii)} & C(r, 0) = \Phi(r)\,, & s_0 \leq r \leq R \\
\text{(iii)} & -DbC_r(R, t) + v_0 C(R, t) = 0\,, & 0 < t < T \\
\text{(iv)} & DbC_r(s(t), t) + v_0 C(s(t), t) & \\
 & \quad = kC(s(t), t) - E & \\
 & \quad = aC(s(t), t)v_s(t)\,, & 0 < t < T \\
\text{(v)} & s(0) = s_0\,, & 0 < s_0 < R
\end{array}
$$

where: $C_r = \partial C/\partial r$, $C_{rr} = \partial^2 C/\partial r^2$, $C_t = \partial C/\partial t$, r is the position coordinate, t the time, and T is the time for which the solution exists. Equation (i) represents 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) (Cushman, 1982). Equation (ii) is the initial condition, and Equation (iii) is the boundary condition on the rhizosphere radius taking into account inter-root competition for the nutrient considered, and a more realistic condition when the more mobile nutrients are considered. Equation (iv) represents the mass nutrient balance conditions at the soil-root interface, and Equation (v) is the initial condition for the free boundary $s(t)$. $v_s(t) = \mathrm{d}s(t)/\mathrm{d}t$ is the rate of radial root growth, a is a stoichiometric coefficient, R is the rhizosphere radius, and s_0 is the initial root radius. The parameter ϵ is given by $\epsilon = v_0 s_0 / Db > 0$. $\Phi(r)$ is the initial concentration profile (given by Equation (11) below). The two free-boundary conditions (1.iv) can be written as:

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

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

where functions g and f are given by:

$$g(C) = \frac{1}{Db}[(k - v_c)C - E] \tag{4}$$

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

which satisfy the following properties:

$$f(C) > 0 \Leftrightarrow C > C_p = \frac{E}{k} \tag{6}$$

$$g(C) > 0 \Leftrightarrow C > C_m = \frac{E}{(k - v_0)}\,, \quad (C_m > C_p) \tag{7}$$

The solution of problem (1) is given by:

$$C(r, t) = \beta(t) - \frac{\alpha(t)}{r^{\epsilon}}\,, \quad s(t) < r < R\,, \quad t > 0 \tag{8}$$

where:

$$\begin{aligned} \alpha(t) &= \left[\frac{E}{Db}\right] \\ &\quad \times \frac{1}{\dfrac{(k - v_0)}{Db}\left[\dfrac{1}{R^{\epsilon}}\alpha_0 - \dfrac{1}{s(t)^{\epsilon}}\right] - \dfrac{\epsilon}{s(t)^{\epsilon+1}}} \\ &= \alpha_2 \frac{s(t)^{\epsilon+1}}{\beta_1 I\left(\dfrac{s(t)}{R}\right) - 1} \end{aligned} \tag{9}$$

$$\begin{aligned} \beta(t) &= \frac{\alpha(t)}{R^{\epsilon}}\left[1 + \frac{s_0}{R}\right] = \alpha_0 \frac{\alpha(t)}{R^{\epsilon}} \\ &= \alpha_0 \frac{\alpha_2}{R^{\epsilon}} \frac{s(t)^{\epsilon+1}}{\beta_1 I\left(\dfrac{s(t)}{R}\right) - 1} \end{aligned} \tag{10}$$

$$\begin{aligned} \Phi(r) &= E \frac{\left[\dfrac{1}{R^{\epsilon}}\left(1 + \dfrac{s_0}{R}\right) - \dfrac{1}{r^{\epsilon}}\right]}{(k - v_0)\left[\dfrac{1}{R^{\epsilon}}\left(1 + \dfrac{s_0}{R}\right)\right] - \dfrac{k}{s_0^{\epsilon}}} \\ &= \alpha(0)\left[\frac{\alpha_0}{R} - \frac{1}{r^{\epsilon}}\right] \\ &= \frac{\beta_2}{\beta_1 I\left(\dfrac{s_0}{R}\right) - 1}\left[\frac{s_0}{r}\right]\epsilon + I\left(\frac{r}{R}\right) \end{aligned} \tag{11}$$

and $s(t)$ is the unique solution of the following Cauchy problem (Ince, 1956; Kreider et al., 1968):

$$\begin{aligned} v_s(t) &= \frac{v_0}{a} L\left(\frac{s(t)}{R}\right), \quad t > 0 \\ s(0) &= s_0 \in (0, R) \end{aligned} \tag{12}$$

where:

$$\begin{aligned} \alpha_2 &= \frac{E}{v_0 s_0}\,, \quad \beta_1 = \frac{R(k - v_0)}{v_0 s_0} > 0\,, \\ \beta_2 &= \frac{RE}{v_0 s_0} > 0\,, \quad \alpha_0 = 1 + \frac{s_0}{R} \end{aligned} \tag{13}$$

$$\begin{aligned} I(x) &= x(\alpha_0 x^{\epsilon} - 1)\,, \\ L(x) &= 1 + \frac{s_0}{R}\frac{1}{I(x)} \quad \text{with } x \in (0, 1) \end{aligned} \tag{14}$$

Moreover, the interface concentration is given by the following expression:

$$C(s(t), t) = \frac{\beta_2 I\left(\dfrac{s(t)}{R}\right)}{\beta_1 I\left(\dfrac{s(t)}{R}\right) - 1}\,, \quad 5 > 0 \tag{15}$$

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

We can remark that the solution, given above, for problem (1) there exists and has a physical meaning if the conditions

$$x_3(w) < \xi < 1\,, \quad \xi = \frac{s_0}{R} \in (0, 1)\,, \tag{16}$$

$$\begin{aligned} \frac{k}{v_0} > \psi(\rho(\xi)) &= \frac{\rho\left(\dfrac{s_0}{R}\right)}{\rho\left(\dfrac{s_0}{R}\right) - 1} = \frac{(1 + \xi)\xi^{\epsilon}}{(1 + \xi)\xi^{\epsilon} - 1}\,, \\ \epsilon = \theta\xi\,, \quad \theta &= \frac{Rv_0}{Db} > 0 \end{aligned} \tag{17}$$

among parameters k/v_0, s_0/R, θ are satisfied (see Appendix A for more details), and $x_3 = x_3(\theta) > 0$ is the unique solution to the equation:

$$\rho(x) = 1\,, \quad x \in (0,1) \tag{18}$$

with:

$$\rho(x) = (1+x)x^{\theta x} \quad \text{with } x \in (0,1)\,, \tag{19}$$

$$\psi(x) = \frac{x}{x-1} \quad \text{with } x \in (1,2)\,. \tag{20}$$

The solution of the Cauchy problem (12) is computed numerically by the Runge-Kutta method for ordinary differential equations (Conte and de Boor, 1972). Figures 1 and 2 represent theoretical results for the interface concentration $C(s(t),t)$ vs. s and the root radius $s(t)$ vs. t as a function of absorption power k for low concentrations and parameters which satisfy condition (17). For simplicity we choose parameter a to equal 1, i.e. we assume that for each ion which arrives at the root only one carrier is available for absorption. Results of a sensitivity analysis using the free-boundary model are shown in Figure 3; the initial values used for the analysis are shown in the same figure. Each parameter has varied between 0.5 and 2.0 of its initial value, whilst all other parameters were held constant at initial values following a methodology similar to that given in Barber (1984).

A similar set of equations for high concentrations is given in the following free-boundary problem assuming that the maximum influx is given by $J \sim J_m$ $(J_m - E > 0)$ if we replace condition (1.iv) with:

$$\begin{aligned} DbC_r(s(t),t) + v_0C(s(t),t) &= J_m - E \\ &= aC(s(t),t)v_s(t)\,, \quad 0 \leqslant t \leqslant T \end{aligned} \tag{21}$$

Now, $f(C)$ and $g(C)$ are given by:

$$g(C) = 1\frac{1}{Db}\,[J_m - E - v_0C] \tag{22}$$

$$f(C) = \frac{J_m - E}{a}\left[\frac{1}{C}\right] \tag{23}$$

which satisfy the following properties:

$$g(C) > 0 \Leftrightarrow C < C_q = \frac{J_m - E}{v_0} \tag{24}$$

$$f(C) > 0\,, \quad \forall C > 0 \tag{25}$$

The solution of the problem for high concentrations is given by:

$$C(r,t) = \gamma(t) - \frac{\delta(t)}{r^{\epsilon}}\,, \quad s(t) < r < R\,, \quad t > 0 \tag{26}$$

where:

$$\begin{aligned} \delta(t) &= \left[\frac{J_m - E}{Db}\right] \\ &\quad \times \frac{1}{\dfrac{v_0}{Db}\left[\dfrac{1}{R^{\epsilon}}\left(1 + \dfrac{s_0}{R}\right) - \dfrac{1}{s(t)^{\epsilon}}\right] + \dfrac{\epsilon}{s(t)^{\epsilon+1}}} \\ &= \frac{J_m - E}{v_0}\,\frac{R^{\epsilon}}{\alpha_0 + \left(\dfrac{R}{s(t)}\right)^{\epsilon}\left(\dfrac{s_0}{s(t)} - 1\right)} \end{aligned} \tag{27}$$

$$\gamma(t) = \frac{\delta(t)}{R^{\epsilon}}\left[1 + \frac{s_0}{R}\right] = \alpha_0\,\frac{\delta(t)}{R^{\epsilon}} \tag{28}$$

$$\Phi(r) = \frac{(J_m - E)}{v_0}\left[1 - \left(\frac{R}{r}\right)^{\epsilon}\frac{1}{\alpha_0}\right] \tag{29}$$

and $s(t)$ is the unique solution to the following Cauchy problem:

$$\frac{\mathrm{d}s(t)}{\mathrm{d}t} = \frac{v_0}{a}\,L\left(\frac{s(t)}{R}\right), \quad s(0) = s_0 \in (0,R)\,, \quad t > 0 \tag{30}$$

where I and L have been defined before. Function $\Phi = \Phi(r)$ satisfies the following conditions

$$\Phi(0^+) = -\infty\,, \quad \Phi(R_1) = \frac{(J_m - E)}{v_0}\,\frac{\xi}{1+\xi} > 0\,,$$

$$\Phi' > 0 \text{ in } (0,R)\,.$$

Moreover, the coefficient $\xi = s_0R$ must verify the condition:

$$\Phi(s_0) = \frac{(J_m - E)}{v_0}\left[1 - \frac{1}{\rho(\xi)}\right] > 0$$

which is equivalent to the condition $x_3(\theta) < \xi =$

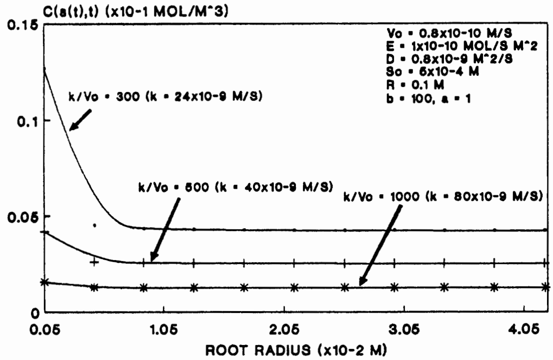

Fig. 1. Interface concentration $C(s(t), t)$ vs. s as a function of absorption power k for low ion concentrations (quasi-stationary method).

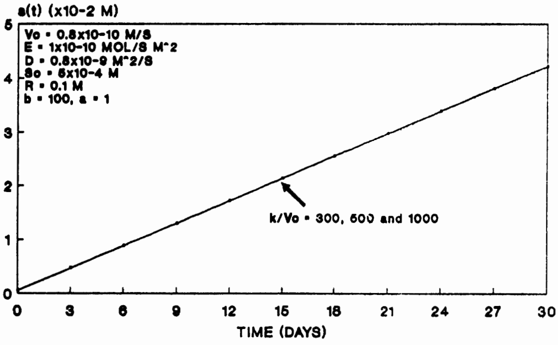

Fig. 2. Root radius $s(t)$ vs. t as a function of absorption power k for low ion concentrations (quasi-stationary method).

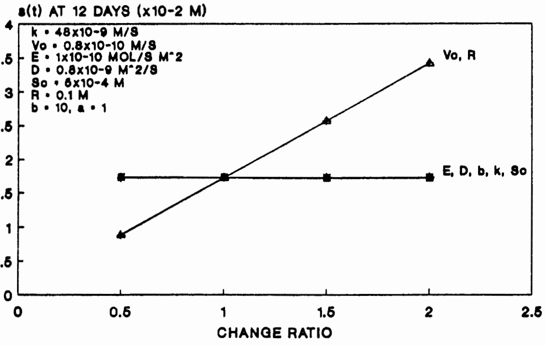

Fig. 3. Results of a sensitivity analysis of parameters for $s(t)$ for low ion concentrations through the quasi-stationary method.

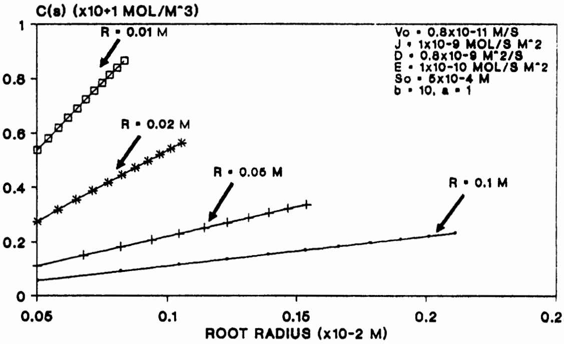

Fig. 4. Interface concentrations $C(s(t), t)$ vs. s as a function of radius R for high ion concentrations (quasi-stationary method).

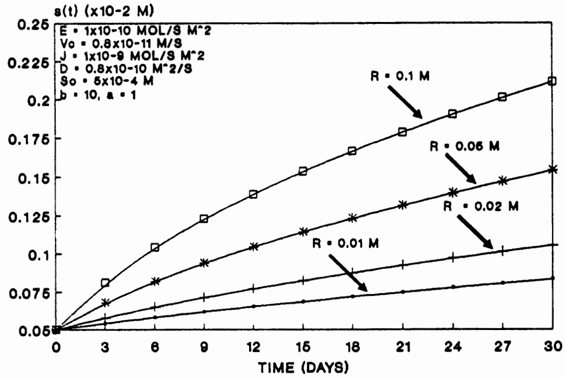

Fig. 5. Root radius $s(t)$ vs. t as a function of radius R for high ion concentrations (quasi-stationary method).

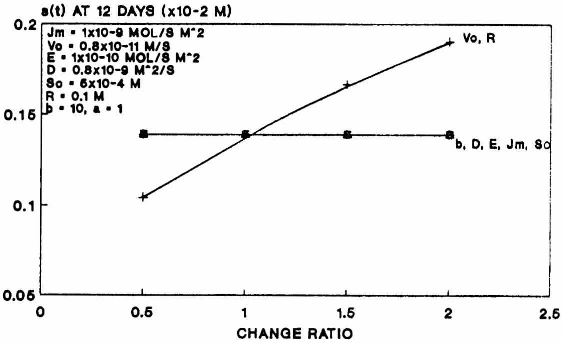

Fig. 6. Results of a sensitivity analysis of parameters for $s(t)$ for high ion concentrations through quasi-stationary method.

$s_0/R < 1$, where $x_3 = x_3(\theta)$ and function ρ have been defined before. Therefore, we find that the interface concentration is given by the following expression:

$$C(s(t), t) = \frac{(J_m - E)}{v_0} \frac{1}{L\left(\frac{s(t)}{R}\right)} = \frac{(J_m - E)}{v_0} \frac{1}{v_s(t)}, \quad t > 0 \tag{31}$$

Moreover, we see that $v_s(t) > 0$, $\forall t > 0$ because $\xi = s_0/R > x_0 = 1/(1+\xi)^{\theta\xi}$ is obviously verified.

The solution of the Cauchy problem (30) is computed numerically by the Runge-Kutta method for ordinary differential equations. Figures 4 and 5 represent theoretical results for the interface concentration $C(s(t), t)$ vs. s and the interface position $s(t)$ vs. t for high concentrations as a function of rhizosphere radius R. Results of a sensitivity analysis using the quasi-stationary method for high concentrations are shown in Figure 6.

In order to compute $C(s(t), t)$ as an explicit function of $s(t)$ and t, and $s(t)$ for a more general of concentrations we propose the following free-boundary problem with conditions (1.iv) given by:

$$DbC_r(s(t), t) + v_0 C(s(t), t) = \frac{kC(s(t), t)}{1 + \frac{kC(s(t), t)}{J_m}} = E = aC(s(t), t)v_s(t), \quad 0 < t < T \tag{32}$$

The two free-boundary conditions $f(C)$ and $g(C)$ can now be written by:

$$g(C) = \frac{1}{Db}\left[\frac{kC}{1 + \frac{k}{J_m}C} E - v_0 C\right] \tag{33}$$

$$f(C) = \frac{1}{a}\left[\frac{k}{1 + \frac{k}{J_m}C} - \frac{E}{C}\right] \tag{34}$$

which satisfy the following properties:

$$g(C) > 0 \Leftrightarrow C_m^- = \frac{-J_m + \delta^2(J_m - E) - d}{2k} < C < C_m^+ = \frac{-J_m + \delta^2(J_m - E) + d}{2k} \tag{35}$$

where $d = \sqrt{[-J_m + \delta^2(J_m - E)]^2 - 4\delta^2 J_m E}$ with the hypothesis: $\delta^2 = k/v_0 > 1$, $E/J_m < (1 - 1/\delta^2)^2$, and

$$f(C) > 0 \Leftrightarrow C > C_p = \frac{E}{k\left[1 - \frac{E}{J_m}\right]} \quad \text{with the hypothesis } \frac{E}{J_m} < 1 \tag{36}$$

The interval (C_m^-, C_m^+) represent the range of concentrations for which $g(C) > 0$ and C_p represent the minimum soil solution concentration required for root growth.

To solve th problem with (32) (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 (Goodman, 1958; Reginato and Tarzia, 1993) to the present case for root growth. The solution is found integrating the partial differential equation (1.i) in r in the domain $(s(t), R)$. Thus:

$$\int_{s(t)}^{R} C_t(r, t)\,\mathrm{d}r = D \int_{s(t)}^{R} C_{rr}(r, t)\,\mathrm{d}r + D(1 + \epsilon) \times \int_{s(t)}^{R} \frac{C_r(r, t)}{r}\,\mathrm{d}r \tag{37}$$

and we propose

$$C(r, t) = \Phi(r)[1 + \eta(t)(R - r)^2] \tag{38}$$

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

$$C(r, 0) = \Phi(r) \Leftrightarrow \eta(0) = 0, \tag{39}$$

$$-DbC_r(R, t) + v_0 C(R, t) = 0 \Leftrightarrow -Db\Phi'(R) + v_0 \Phi(R) = 0. \tag{40}$$

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

$$\begin{aligned}\nu(t) &= C(s(t), t) \\ &= \Phi(s(t))[1 + \eta(t)(R - s(t))^2] \qquad (41)\end{aligned}$$

which depends on the parameters of the system through $s(t)$, $\Phi(s(t))$ and $\eta(t)$. Replacing (40) and (41) in Equation (37), after some elementary manipulations, the problem reduces to:

$$\int_{s(t)}^{R} C_t(r, t)\,\mathrm{d}r = D[C_r(R, t) - g(\nu(t))]$$

$$+ D(1 + \epsilon)\left[\frac{C(R, t)}{R} - \frac{\nu(t)}{s(t)} + \int_{s(t)}^{R} \frac{C(r, t)}{r^2}\,\mathrm{d}r\right]$$

$$v_s(t) = f(\nu(t))\,, \quad s(0) = s_0\,, \quad t > 0\,. \qquad (42)$$

Replacing (38) in Equation (42), after some elementary manipulations we obtain the following system of two coupled ordinary differential equations (see Appendix B) (valid for the cases $\epsilon \neq 1, 2, 3$):

$$\frac{\mathrm{d}\eta(t)}{\mathrm{d}t} = \frac{F_1 + F_2 + D(1 + \epsilon)(F_3 + F_4 + F_5 + F_6 + F_7 + F_8)}{(F_9 + F_{10} + F_{11})}$$

$$\eta(0) = 0$$

$$\frac{\mathrm{d}s(t)}{\mathrm{d}t} = \frac{1}{a}\left[\frac{k}{1 + \frac{k}{J_m}\Phi(s(t))[1 + \eta(t)(R - s(t))^2]} - \frac{E}{\Phi(s(t))[1 + \eta(t)(R - s(t))^2]}\right] = f(\nu(t))\,,$$

$$s(0) = s_0 \qquad (43)$$

and

$$\Phi(r) = BA - \frac{A}{r^\epsilon} \quad \text{with } B = \frac{1}{R^\epsilon}\left[1 + \frac{s_0}{R}\right],$$

$$A = \frac{E}{(k - v_0)B - \frac{k}{s_0^\epsilon}} \qquad (44)$$

which verifies conditions (39) and (40).

The initial profile concentration $\Phi(r)$ given by Equation (44) above has been computed by the quasi-stationary method (Reginato et al., 1990) for low concentrations and it is determinated by the system. The functions F_i are given by:

$$F_1 = \left[\frac{v_0}{b} + \frac{D(1 + \epsilon)}{R}\right]\frac{As_0}{R^{\epsilon+1}}\,,$$

$$F_2 = -\frac{1}{b}\left[\frac{k\Phi(s(t))[1 + \eta(t)(R - s(t))^2]}{1 + \frac{k}{J_m}\Phi(s(t))[1 + \eta(t)(R - s(t))^2]} - E - v_0\Phi - v_0\Phi(s(t))[1 + \eta(t)(R - s(t))^2]\right]$$

$$= -Dg(g(\nu(t))$$

$$F_3 = -\frac{\Phi(s(t))[1 + \eta(t)(R - s(t))^2}{s(t)}$$

$$F_4 = AB[1 + \eta(t)R^2]\left[\frac{1}{s(t)} - \frac{1}{R}\right],$$

$$F_5 = 2AB\eta(t)R\ln\left[\frac{R}{s(t)}\right] + AB\eta(t)[R - s(t)]$$

$$F_6 = -\frac{A[1 + \eta(t)R^2]}{(\epsilon + 1)}\left[\frac{1}{s^{(\epsilon+1)}(t)} - \frac{1}{R^{(\epsilon+1)}}\right]$$

$$F_7 = \frac{2}{\epsilon}A\eta(t)R\left[\frac{1}{s^\epsilon(t)} - \frac{1}{R^\epsilon}\right]$$

$$F_8 = \frac{A\eta(t)}{(1 - \epsilon)}\left[\frac{1}{s^{(\epsilon-1)}(t)} - \frac{1}{R^{(\epsilon-1)}}\right],$$

$$F_9 = ABR^2[R - s(t)] - \frac{AR^2}{(1 - \epsilon)}[R^{(1-\epsilon)} - s^{(1-\epsilon)}(t)]$$

$$F_{10} = -ABR[R^2 - s^2(t)] + \frac{2AR}{(2 - \epsilon)}[R^{(2-\epsilon)} - s^{(2-\epsilon)}(t)]\,,$$

$$F_{11} = \frac{AB}{3}[R^3 - s^3(t)] - \frac{A}{(3 - \epsilon)}[R^{(3-\epsilon)} - s^{(3-\epsilon)}(t)]$$

We can remark that for the particular cases $\epsilon = 1$, 2 and 3, a similar system to (43) of two ordinary differential equations can be obtained.

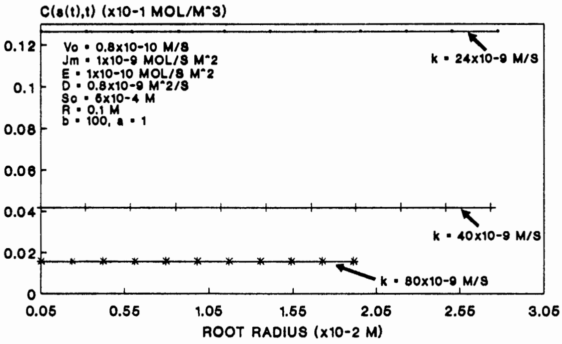

Fig. 7. Interface concentration $C(s(t), t)$ vs. s as a function of absorption power k for low ion concentrations through integral balance.

The solution of system (43) is computed numerically by the Runge-Kutta method for a system of ordinary differential equations. Figures 7 and 8 represent theoretical results for the interface concentration $C(s(t), t)$ vs. s and the interface position $s(t)$ vs. t as a function of absorption power k in the range of low concentrations and parameters which satisfy condition (17). Results of a sensitivity analysis using the balance integral method for low concentrations are shown in Figure 9.

For high concentrations we obtain quite a similar system of ordinary differential equations with the initial profile of concentrations (computed by the quasi-stationary method for high concentrations) given by:

$$\Phi(r) = BA - \frac{A}{r^{\epsilon}} \tag{45}$$

where:

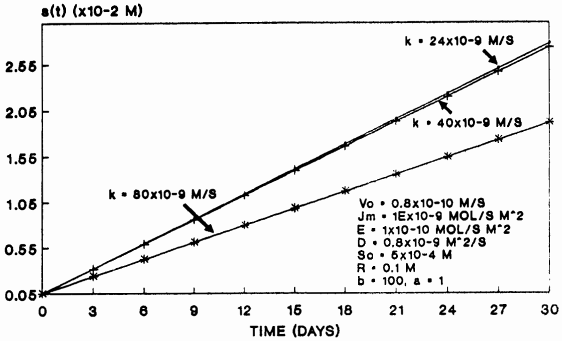

Fig. 8. Root radius $s(t)$ vs. t as a function of absorption power k for low ion concentrations (integral balance).

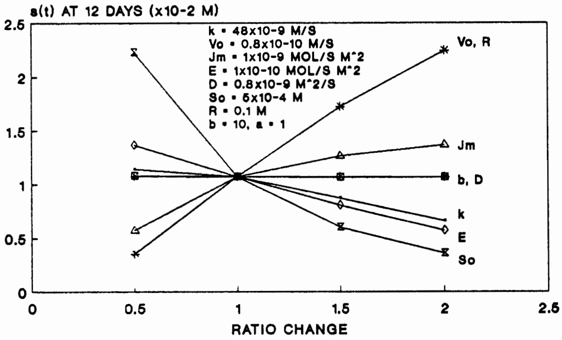

Fig. 9. Results of a sensitivity analysis of parameters for $s(t)$ through the balance integral method for low ion concentrations.

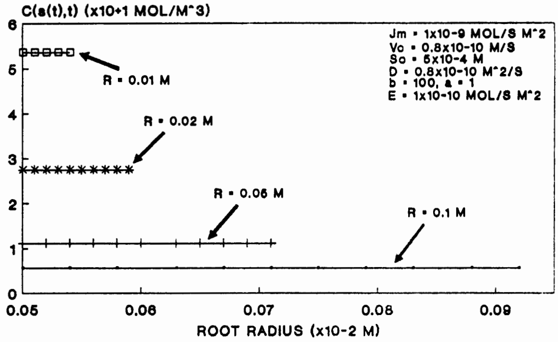

Fig. 10. Interface concentration $C(s(t), t)$ vs. s as a function of parameter R for high ion concentrations (integral balance).

$$B = \frac{1}{R^{\epsilon}}\left(1 + \frac{s_0}{R}\right), \quad A = \frac{J_m - E}{\dfrac{v_0}{R^{\epsilon}}\left(1 + \dfrac{s_0}{R}\right)} = \frac{J_m - E}{Bv_0}$$

Figures 10 and 11 represent theoretical results for $C(s(t), t)$ vs. s and $s(t)$ vs. t, respectively, as a function of rhizosphere radius R in the range of high concentrations, and Figure 12 represents the results of sensitivity analysis for predicted root growth through the balance integral method for high concentrations.

Conclusions

From the analysis of the results given by the quasi-stationary method, we conclude that for low concentrations the results of sensitivity analysis indicate that predicted $s(t)$ increases rapidly

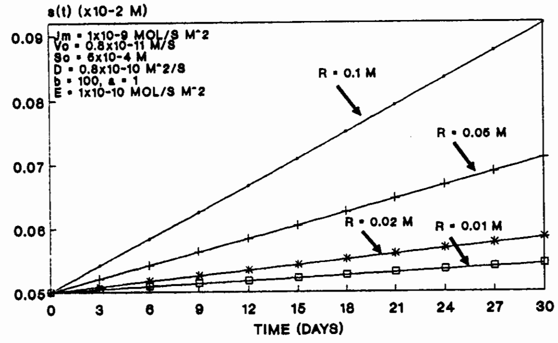

Fig. 11. Root radius $s(t)$ vs. t as a function of radius R for high ion concentrations (integral balance).

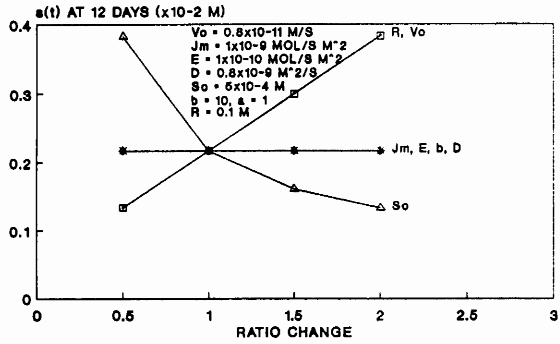

Fig. 12. Results of sensitivity analysis of parameters for $s(t)$ through the balance integral method for high ion concentrations.

with increases in v_0 and R (Fig. 3). Values for k, b, D, E, and s_0 had little or no effect because the mathematical approximation of the method is poor. On the other hand, for low concentrations the results of sensitivity analysis obtained for the balance integral method (Fig. 9) likewise indicate that predicted $s(t)$ increases rapidly with v_0 and R. The increase in v_0 represents an increase in total nutrient available for the plant, since, if the remaining parameters are held constant, increasing v_0 increases the convective flux to root. Increasing R increases the rhizosphere volume and so a greater ion quantity is available. At the same time we conclude that the predicted $s(t)$ increases moderately with J_m. Values of b and D had little or no effect, whilst increasing k, E, and s_0 decreases the predicted $s(t)$. The decrease with k (Fig. 8) occurs because the gradient at root-soil interface (given by Equation (4)) as a function of k and $C(s)$ decreases. The expression $g(C(s(t), t) = 1/Db[(k - v_0)C(s(t), t) - E]$ takes into account the combined effects of the increase in k and the decrease of $C(s(t), t)$ as a function of k (Fig. 7). The decrease with s_0 occurs because, although the root surface increases as s_0^2, the rhizosphere volume available decreases as $L(R^2 - s_0^2)$ where L is the length root and, taking into account that $R \gg s_0$, then $(R^2 - s_0^2) > s_0^2$. No allowance for a change in L with time is made because we have only considered radial growth.

From the analysis of the results obtained by the quasi-stationary method, the interface concentration becomes nearly constant after a week elapsed (Compare Figs. 1 and 2), whilst from the results obtained by the balance integral method the interface concentration is constant throughout the period simulated (Fig. 7) in agreement with De Willigen's results (1981) on N uptake. From the analysis of the results obtained by the quasi-stationary method and the balance integral method for high concentrations, the results of sensitivity analysis indicate that predicted $s(t)$ increases rapidly with increases in v_0 and R (Figures 6 and 12). Values for b, D, E and J_m had little or no effect. The predicted $s(t)$ decreased with respect to s_0.

By comparing the results obtained by the quasi-stationary method and the balance integral method we can conclude that: firstly, the mathematics of the quasi-stationary method allow analytical expressions which must be satisfied by the system parameters, such as inequality (17), and secondly the general qualitative behaviour of the results is similar for both methods, although the balance integral method gives us more detailed theoretical information with respect to dependence on system parameters. For example, for low concentrations, the variation of $s(t)$ vs. t with respect to the parameter k is negligible for the quasi-stationary method (Fig. 3), whilst the balance integral method gives us an appreciable change (Fig. 9).

In conclusion, this paper represents a qualitative approach for the effects on root growth due to absorption of only one mobile nutrient. From comparison between the results of the present model and the model for ions that are relatively immobile for low and high concentrations (Reginato et al., 1990, 1991) we conclude that the efficiency of absorption kinetics

($J = kC$ or $J = J_m$, respectively) is greater for low concentrations for both models. Moreover, these models are useful as a basis for developing more complex models for transport of nutrients and their effect on root growth. For example, these same models take into account the root length (the effects of some parameters could be changed) and simultaneous absorption of one or more immobile and mobile ions.

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Appendix A

Nomenclature

r:	Position (radius) coordinate	(cm)
t:	Time	(Sec)
J_m:	Rate of influx at infinite concentration	$\left(\frac{\text{Mol}}{\text{Sec-cm}^2}\right)$
K_m:	Michaelis Menten constant	$\left(\frac{\text{Mol}}{\text{cm}^3}\right)$
k:	Absorption power of root	$\left(\frac{\text{cm}}{\text{Sec}}\right)$
v_0:	Flux velocity of soil solution at root surface	$\left(\frac{\text{cm}}{\text{Sec}}\right)$
D:	Effective diffusion coefficient	$\left(\frac{\text{cm}^2}{\text{Sec}}\right)$
C:	Total diffusible ion concentration	$\left(\frac{\text{Mol}}{\text{cm}^3}\right)$
C_1:	Ion concentration in soil solution	$\left(\frac{\text{Mol}}{\text{cm}^3}\right)$
$C(s(t), t)$:	Ion concentration in soil solution at root-soil interface	$\left(\frac{\text{Mol}}{\text{cm}^3}\right)$
$\Phi(r)$:	Initial soil solution concentration profile	$\left(\frac{\text{Mol}}{\text{cm}^3}\right)$
s_0:	Initial radius	(cm)
E:	Constant efflux	$\left(\frac{\text{Mol}}{\text{Sec-cm}^2}\right)$
$s(t)$:	Instantaneous root radius	(cm)
$v_s(t)$:	Rate of radial root growth	$\left(\frac{\text{cm}}{\text{Sec}}\right)$

L:	Root length	(cm)
R:	Rhizosphere radius	(cm)
b:	Buffer power	Dimensionless
a:	Stoichiometric coefficient	Dimensionless
ϵ:	Parameter	Dimensionless
α_1:	Parameter	$\left(\frac{1}{\text{cm}}\right)$
α_2:	Parameter	$\left(\frac{\text{Mol}}{\text{cm}^4}\right)$
$\alpha(t), \delta(t)$	Coefficients	$\left(\frac{\text{Mol}}{\text{cm}^2}\right)$
$\beta(t), \gamma(t), \nu(t)$	Coefficients	$\left(\frac{\text{Mol}}{\text{cm}^3}\right)$
$\eta(t)$	Coefficient	$\left(\frac{1}{\text{cm}^2}\right)$

Appendix B

Part A (quasi-stationary method)

The expression for $C(r,t)$ and $s(t)$ can be obtained by a method similar to that developed in Reginato et al. (1990). Function I, given by (14), satisfies the following properties:

$$I(0)=0\,, \qquad I(x_0)=0 \qquad I(1)=\frac{s_0}{R}$$

$$I<0 \text{ in } (0,x_0)\,, \quad I>0 \text{ in } (x_0,1)\,, \quad I'>0 \text{ in } [x_0,1]$$

$$I'(x_1)=0\,, \qquad I(x_1)=-\frac{\epsilon}{\epsilon+1}x_1$$

$$I'<0 \text{ in } (0,x_1)\,,\ I'>0 \text{ in } (x_1,1)$$

$$\epsilon \leqslant I'(x) \leqslant \mu = \epsilon + (1+\epsilon)\frac{s_0}{R} \text{ in } (x_0,1)\,,$$

where:

$$x_0=\frac{1}{(\alpha_0)^{1/\epsilon}}\,, \quad \alpha_0 = 1+\frac{s_0}{R}\,, \quad \epsilon=\frac{v_0 s_0}{Db}=\theta\,\frac{s_0}{R}\,,$$

$$0<x_1=\frac{1}{((1+\epsilon)\alpha_0)^{1/\epsilon}}<x_0$$

Owing to ($\xi = s_0/R \in (0,1)$):

$$\beta_1 I\left(\frac{s(t)}{R}\right)-1=\frac{k-v_0}{v_0}\frac{1}{\xi}I\left(\frac{s(t)}{R}\right)-1 \geqslant \frac{k-v_0}{v_0}\frac{I(\xi)}{\xi}-1>0\,,$$
$$\forall t>0$$

condition (17) is a consequence of the following equivalences:

$$\beta_1 I\left(\frac{s(t)}{R}\right)-1>0,\ \forall t>0 \Leftrightarrow \frac{k}{k-v_0}<\rho(\xi)<2$$
$$\text{with } \xi \in (0,1) \Leftrightarrow$$

$$\Leftrightarrow \frac{k}{v_0}>\frac{\rho(\xi)}{\rho(\xi)-1}=\psi(\rho(\xi))$$
$$\text{with } \rho(\xi)\in(1,2)\Leftrightarrow$$

$$\Leftrightarrow \frac{k}{v_0}>\psi(\rho(\xi))$$
$$\text{with } x_3(\theta)<\xi<1$$

where $x_3 = x_3 > 0$ is the unique solution to the equation $\rho(x)=1$ with $x \in (0,1)$.

Moreover, function $\rho=\rho(x)$ verifies the following conditions:

$$\rho(0^+)=1,\ \rho(1)=2$$

$$\rho'>0 \text{ in } (x_4(\theta),1)\,, \qquad \rho'<0 \text{ in } (0,x_4(\varrho))$$

$$\exists! x_4 = x_4(\theta)\in(0,1) \quad \text{such that } \rho'(x_4)=0\,, \quad \rho''(x_4)>0$$

$$\exists! x_3 = x_3(\theta)\in(x_4,1) \quad \text{such that } \rho(x_3)=1$$

Then the solution to the ordinary differential equation (12) is well defined, because

$$|\mathrm{L}'(\mathrm{x})| \leqslant \frac{(\mathrm{k}-v_0)^2}{v_0^2 \mathrm{s}_0}\mathrm{R}\mu\,, \quad \forall \mathrm{x}\in[\mathrm{x}_0,1]\,.$$

Part B (Integral balance)

Replacing (38) in Equation (42), after some manipulations, we obtain:

$$\int_{s(t)}^{R} C_t(r,t)\,\mathrm{d}r = \int_{s(t)}^{R} \Phi(r)\dot{\eta}(t)[R_1-r]^2\,\mathrm{d}r$$
$$= R^2\dot{\eta}(t)\int_{s(t)}^{R}\Phi(r)\,\mathrm{d}r - 2R\dot{\eta}(t)\int_{s(t)}^{R} r\Phi(r)\,\mathrm{d}r$$
$$+\dot{\eta}(t)\int_{s(t)}^{R}\Phi(r)r^2\,\mathrm{d}r$$

and, taking into account (44), we obtain:

$$\int_{\mathrm{s(t)}}^{\mathrm{R}}\Phi(r)\,\mathrm{d}r = AB\int_{s(t)}^{R}\mathrm{d}r - A\int_{s(t)}^{R} r^{-\epsilon}\,\mathrm{d}r$$
$$= AB[R-s(t)] - \frac{A}{(1-\epsilon)}[R^{(1-\epsilon)}-s^{(1-\epsilon)}(t)]\,, \qquad \text{(with } \epsilon \neq 1\text{)}$$

$$\int_{s(t)}^{R} r\Phi(r)\,\mathrm{d}r = AB\int_{s(t)}^{R} r\,\mathrm{d}r - A\int_{s(t)}^{R} r^{(1-\epsilon)}\,\mathrm{d}r$$
$$=\frac{AB}{2}[R^2-s^2(t)]$$
$$-\frac{A}{(2-\epsilon)}[R^{(2-\epsilon)}-s^{(2-\epsilon)}(t)]\,, \qquad \text{(with } \epsilon \neq 2\text{)}$$

$$\int_{s(t)}^{R} r^2\Phi(r)\,\mathrm{d}r = AB\int_{s(t)}^{R} r^2\,\mathrm{d}r - A\int_{s(t)}^{R} r^{(2-\epsilon)}\,\mathrm{d}r$$
$$= \frac{AB}{3}[R^3 - s^3(t)]$$
$$- \frac{A}{(3-\epsilon)}[R^{(3-\epsilon)} - s^{(3-\epsilon)}(t)]\,, \quad (\text{with } \epsilon \neq 3)$$

then:

$$\int_{s(t)}^{R} C_t(r,t)\,\mathrm{d}r = R^2\dot{\eta}(t)AB[R - s(t)] - \frac{AR^2\dot{\eta}(t)}{(1-\epsilon)}$$
$$\times [R^{(1-\epsilon)} - s^{(1-\epsilon)}(t)] - 2R\dot{\eta}(t)\frac{AB}{2}[R^2 - s^2(t)]$$
$$+ \frac{A2R\dot{\eta}(t)}{(2-\epsilon)}[R^{(2-\epsilon)} - s^{(2-\epsilon)}(t)]$$
$$+ \dot{\eta}(t)\frac{AB}{3}[R^3 - s^3(t)] - \frac{A\dot{\eta}(t)}{(3-\epsilon)}[R^{(3-\epsilon)} - s^{(3-\epsilon)}(t)]\,. \tag{B.1}$$

Similarly, we obtain:

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

$$\int_{s(t)}^{R} \frac{C(r,t)}{r^2}\,\mathrm{d}r = AB[1 + \eta(t)R^2]\left[\frac{1}{s(t)} - \frac{1}{R}\right]$$
$$- 2AB\eta(t)R\ln\frac{R}{s(t)} - AB\eta(t)[R - s(t)]$$
$$- \frac{A[1 + \eta(t)R^2]}{(1+\epsilon)}\left[\frac{1}{s^{(\epsilon+1)}(t)} - \frac{1}{R^{(\epsilon+1)}}\right]$$
$$- \frac{2A\eta(t)R}{\epsilon}\left[\frac{1}{s^\epsilon(t)} - \frac{1}{R^\epsilon}\right]$$
$$- \frac{A\eta(t)}{(1-\epsilon)}\left[\frac{1}{R^{(\epsilon-1)}} - \frac{1}{s^{(\epsilon-1)}(t)}\right] \tag{B.2}$$

Finally, replacing (B.1) and (B.2) in Equation (42), after elementary manipulations, we obtain the system (43).