

MASS FLOW AND DIFFUSION OF NUTRIENTS TO A ROOT WITH CONSTANT OR ZERO-SINK UPTAKE I. CONSTANT UPTAKE

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This paper deals with transport of nutrients in soil by mass flow and diffusion towards plant roots. The root system is assumed to consist of uniformly distributed cylindrical vertical parallel roots, all taking up nutrients at the same constant rate. Each root thus can be thought to be surrounded by a separate soil cylinder. Steady-state conditions with respect to flow of water to the root are assumed. Two situations with respect to the steady-state water flow are distinguished: one where replenishment of the water taken up by the root takes place at the outer boundary of the soil cylinder, and one where replenishment takes place uniformly over the soil cylinder. Analytical solutions to the transport problem are derived. The constant uptake condition leads to concentration distributions converging eventually to a steady-rate solution, where the decrease in concentration is independent of time. With these, the period of unconstrained uptake T_u , i.e., the period during which transport in the soil allows the required uptake, is calculated. It is shown that transport by mass flow is more important the stronger the nutrients are adsorbed by the soil. The solutions for the two situations of steady-state water flow are shown to differ only slightly.

Since Barber (1962), it has generally been accepted that nutrients are transported toward the plant root by two mechanisms: transport by mass flow, generated by the uptake of water by the plant root, and transport by diffusion, whenever the concentration in the soil solution is not equal to the ratio of the actual rates of nutrient and water uptake.

Current models on uptake of nutrients by roots describe uptake as governed principally by the concentration of the soil solution (Nye and Tinker 1977; Barber 1984; Jungk and Claassen 1986). For conditions where nutrient supply to

the root is not limiting uptake, this approach may vastly overestimate uptake (Barraclough 1986). There is ample evidence for regulation of nutrient uptake (Pitman 1976; Loneragan 1978), especially in the case of the macronutrients N, P, and K, though regulation is not complete and instantaneous (Clarkson 1985). The starting point for our discussions, therefore, is that uptake is determined by plant demand, i.e. the rate of dry matter production times required nutrient content. Uptake by the roots is assumed to be in accordance with plant demand, as long as transport in the soil will maintain the concentration at the root surface above a certain limiting concentration. This limiting concentration is virtually zero for most conditions found in agricultural practice (De Willigen and Van Noordwijk, 1987). We will assume that, if plant demand cannot be met, the root will behave as a zero sink, i.e., its uptake rate then equals the rate at which nutrients arrive at the root surface. In our description, the root thus either takes up at the required rate, as long as the soil can maintain a sufficiently high transport rate of the nutrient to the root, or it takes up at the same rate at which the nutrient arrives at its surface. This approach is similar to that suggested by Olsen and Kemper (1968).

The goal of this paper is twofold: first, to solve equations describing transport by mass flow and diffusion on a microscopic scale around a single root, for constant sink uptake and second, to show how the equations derived can be used on a macroscopic scale (i.e., in crop growth simulation models). Solutions to the transport equation for nutrient flow for an idealized distribution of roots in the soil will be presented and discussed. The assumed simple distribution and orientation of roots leads to a simple geometry of the region for which the equations can be solved and allows to limit the attention to a single root and its vicinity. More complex geometries can be considered by reference to this simplified situation.

Nutrient demand of agricultural crops during a major part of the growing season can be taken to be constant (De Willigen and Van Noordwijk

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Received March 9, 1993; accepted Sept. 10, 1993.

1987, Van Noordwijk et al. 1990). For the conditions chosen here this also means a constant uptake rate per root, each root being confined to an equal volume of soil. The uptake potential of such a root can be characterized by a characteristic time: the period during which the concentration at the root surface exceeds the limiting (in practice zero-) concentration or, to put it differently, the period during which uptake is in accordance with plant demand. This characteristic time will in the following be called the period of unconstrained uptake and will be indicated by the symbol T_u (days), or t_u (dimensionless units). The constant uptake condition will be treated in this paper.

TRANSPORT EQUATION, BOUNDARY AND INITIAL CONDITIONS

Transport equation

The governing equation for transport of a nutrient by mass flow and diffusion, subject to linear adsorption, in a homogeneous soil of constant water content reads in cylindrical

cal coordinates:

$$(K_a + \theta) \frac{\partial C}{\partial T} = \frac{1}{R} \frac{\partial}{\partial R} RD \frac{\partial C}{\partial R} - \frac{1}{R} \frac{\partial}{\partial R} RVC \quad (1)$$

where C is the concentration in the soil solution (mg cm^{-3}), T is time [days], R is radial distance from root center (cm), K_a is the adsorption constant [ml cm^{-3}], θ is the soil water content [ml cm^{-3}], D is the diffusion coefficient [$\text{cm}^2 \text{day}^{-1}$], and V is the flux of water towards the root [cm day^{-1}]. It will be assumed here that D is constant and that a steady-state situation exists with respect to flux of water, i.e., V is only a function of R and not of T .

Geometry of soil/root system and boundary conditions

Consider a uniformly distributed parallel root system with root density L_{rv} cm cm^{-3} , and suppose all roots have the same length H cm and radius R_0 cm (Table 1 gives a list of symbols). To each root, therefore, a hexagonal cylinder

TABLE 1
List of symbols

Symbol	Name	Dimension	Dimensionless symbol
T	time	d	$t = DT/R_0^2$
T_u	period of unconstrained uptake	d	$t_u = DT_u/R_0^2$
$T_{u,\max}$	maximum T_u	d	$t_{u,\max}$
R	radial coordinate	cm	$r = R/R_0$
R_0	root radius	cm	
R_1	soil cylinder radius	cm	$\rho = R_1/R_0$
H	root length	cm	$\eta = H/R_0$
A	plant demand for nutrients	$\text{mg} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$	$\omega_u = -\rho^2 B / (2\phi\eta)$
S_i	initial amount of nutrient	$\text{mg} \cdot \text{cm}^3$	
ϕ	supply/demand parameter		$\phi = DS_i / (AR_0)$
C	concentration	$\text{mg} \cdot \text{ml}^{-1}$	$c = C/C_i$
C_i	initial concentration	$\text{mg} \cdot \text{ml}^{-1}$	
$B = K_a + \theta$	buffer capacity	$\text{ml} \cdot \text{cm}^{-3}$	$\beta = (K_a + \theta) / \theta$
E	transpiration rate	$\text{cm} \cdot \text{d}^{-1}$	
V	flux of water	$\text{cm} \cdot \text{d}^{-1}$	$\mu = E / \{2\pi HDL_{rv}(\rho^2 - 1)\}$ $\nu = -E / (2\pi HDL_{rv})$
L_{rv}	root density	$\text{cm} \cdot \text{cm}^{-3}$	
K_a	adsorption constant	$\text{ml} \cdot \text{cm}^{-3}$	
θ	water content	$\text{ml} \cdot \text{cm}^{-3}$	
D	diffusion coefficient	$\text{cm}^2 \cdot \text{d}^{-1}$	

can be assigned, which can be approximated by a radial cylinder of height H and radius R_1 , the latter given by:

$$R_1 = \frac{1}{\sqrt{\pi L_{rv}}} \quad (2)$$

From the assumed geometry it follows that the boundary condition at the outer boundary is that of vanishing nutrient flux F :

$$R = R_1, \quad F = 0 \quad (3)$$

The boundary condition for nutrient transport at the root surface is that of constant flux (generated by the constant plant demand). If the plant demand amounts to A mg/(cm² day⁻¹), each root has to take up A/L_{rv} mg day⁻¹. The condition at the root surface accordingly reads:

$$R = R_0, \quad F = -\frac{A}{2\pi L_{rv} H R_0} \quad (4)$$

Initial condition

The chosen initial condition is that of constant concentration:

$$T = 0, \quad C = C_i \quad (5)$$

Steady-state water flux

In earlier discussions of the combined effects of mass flow and diffusion (Nye and Marriott 1969; Cushman 1980; De Willigen 1981; De Willigen and Van Noordwijk 1987), it has been assumed that water content in the soil cylinder around a root is constant and that the water taken up by the root is replenished from outside the soil cylinder. Such a description may overestimate the effects of mass flow. As an alternative description, we will consider here also uniform replenishment within the soil cylinder.

Replenishment from Outside the Soil Cylinder

The flux of water V at distance R can in this case be given by (De Willigen and Van Noordwijk 1987):

$$V = -\frac{E}{2\pi H R L_{rv}} = -\frac{E R_1^2}{2HR} \quad (6)$$

Substitution of (6) into (1) yields:

$$(K_a + \theta) \frac{\partial C}{\partial T} = D \frac{\partial^2 C}{\partial R^2} + \frac{R_1^2 E + 2DH}{2HR} \frac{\partial C}{\partial R} \quad (7)$$

and the boundary conditions (3) and (4) become:

$$R = R_1, \quad D \frac{\partial C}{\partial R} + \frac{R_1 E}{2H} C = 0 \quad (8)$$

$$R = R_0, \quad D \frac{\partial C}{\partial R} + \frac{R_1^2 E}{2HR_0} C = \frac{A}{2\pi H R_0 L_{rv}} \quad (9)$$

Uniform Replenishment in the Soil Cylinder

In macroscopic models of water and/or nutrient uptake the soil profile usually is divided vertically into a number of layers that normally have a thickness of 10–20 cm each (e.g., Penning de Vries et al. 1989). Within such a layer no vertical gradients in water content exist. The difference between inflow and outflow of water is supposed to contribute uniformly to the change of water content in this layer. For such a layer, a steady-state situation with respect to radial flow of water is considered here, where the loss of water attributable to uptake by the root is continuously replenished. The flux in such a situation can be given as (De Willigen and Van Noordwijk 1987):

$$V = \frac{R_1^2 E}{2H(R_1^2 - R_0^2)} \left\{ \frac{R^2 - R_1^2}{R} \right\} \quad (10)$$

when (10) is substituted in (1), this results in:

$$(K_a + \theta) \frac{\partial C}{\partial T} = D \frac{\partial^2 C}{\partial R^2} + \frac{(R_1^2 - R^2) R_1^2 E + 2DH(R_1^2 - R_0^2)}{2H(R_1^2 - R_0^2)R} \frac{\partial C}{\partial R} - \frac{R_1^2 E}{H(R_1^2 - R_0^2)} C \quad (11)$$

while the boundary conditions (3) and (4) become:

$$R = R_1, \quad \frac{\partial C}{\partial R} = 0 \quad (12)$$

$$R = R_0, \quad D \frac{\partial C}{\partial R} + \frac{R_1^2 E}{2HR_0} C = \frac{A}{2\pi H R_0 L_{rv}} \quad (13)$$

Dimensionless variables

To facilitate notation and to show the interrelation between the various parameters and variables, dimensionless quantities are defined as given in Table 1. Variables and parameters with dimension are denoted by capital Roman letters, dimensionless variables by lower case

Roman letters, and dimensionless parameters where by Greek letters.

Replenishment from Outside the Soil Cylinder

Use of dimensionless variables and parameters transforms (7)–(9) into:

$$B \frac{\partial c}{\partial t} = \frac{\partial^2 c}{\partial r^2} + \frac{1 - 2\nu}{r} \frac{\partial c}{\partial r} \quad (14)$$

$$r = \rho, \quad -\frac{\partial c}{\partial r} + \frac{2\nu}{\rho} c = 0 \quad (15)$$

$$r = 1, \quad -\frac{\partial c}{\partial r} + 2\nu c = -\frac{\rho^2 B}{2\phi\eta} = \omega_u \quad (16)$$

Uniform Replenishment in the Soil Cylinder

Equations (10)–(12) transform into:

$$B \frac{\partial c}{\partial t} = \frac{\partial^2 c}{\partial r^2} + \frac{1 + \mu(\rho^2 - r^2)}{\rho^2} \frac{\partial c}{\partial r} - 2\mu c \quad (17)$$

$$r = \rho, \quad \frac{\partial c}{\partial r} = 0 \quad (18)$$

$$r = 1, \quad -\frac{\partial c}{\partial r} + \mu(1 - \rho^2)c = \omega_u \quad (19)$$

Initial Condition

The initial condition (5) transforms into:

$$t = 0, \quad c = 1 \quad (20)$$

SOLUTIONS

Replenishment from outside soil cylinder

The solution for (14)–(16) with (20) was derived by De Willigen (1981); it reads:

$$c = \frac{(\rho^2 - 1)(\nu + 1)r^{2\nu}}{\rho^{2\nu+2} - 1} \quad (a)$$

$$+ \omega_u \frac{2(\nu + 1)r^{2\nu} t}{\rho^{2\nu+2} - 1} B \quad (b)$$

$$+ \omega_u \left\{ \frac{r^{2\nu}(r^2 - \rho^2)}{2(\rho^{2\nu+2} - 1)} + \frac{\rho^2(\rho^{2\nu} - r^{2\nu})}{2\nu(\rho^{2\nu+2} - 1)} \right. \quad (21)$$

$$+ \frac{\rho^2(\rho^{2\nu} - 1)r^{2\nu}(\nu + 1)}{2\nu(\rho^{2\nu+2} - 1)^2} \quad (c)$$

$$\left. + \frac{r^{2\nu}(\nu + 1)(1 - \rho^{2\nu+4})}{(2\nu + 4)(\rho^{2\nu+2} - 1)^2} \right\}$$

$$+ (\omega_u - 2\nu)r^\nu \pi \sum_{n=1}^{\infty} \frac{J_{\nu+1}(\alpha_n)J_{\nu+1}(\rho\alpha_n)}{\alpha_n} \quad (d)$$

$$F_\nu(r, \alpha_n) \exp\left(\frac{-\alpha_n^2 t}{B}\right) \quad (d)$$

$$+ \frac{2\nu r^\nu \pi}{\rho^{\nu+1}} \sum_{n=1}^{\infty} \frac{J_{\nu+1}^2(\alpha_n)}{\alpha_n} \quad (e)$$

$$F_\nu(r, \alpha_n) \exp\left(\frac{-\alpha_n^2 t}{B}\right) \quad (e)$$

$$F_\nu(r, \alpha_n) = \frac{Y_{\nu+1}(\rho\alpha_n)J_\nu(r\alpha_n) - Y_\nu(r\alpha_n)J_{\nu+1}(\rho\alpha_n)}{J_{\nu+1}^2(\alpha_n) - J_{\nu+1}^2(\rho\alpha_n)},$$

and α_n is the n th root of $Y_{\nu+1}(\rho\alpha)J_\nu(\alpha) - Y_\nu(\alpha)J_{\nu+1}(\rho\alpha) = 0$. J_ν and Y_ν are the Bessel function and modified Bessel function, respectively, of the first kind and order ν .

In (21), four parts can be distinguished: the first part (21a) gives the steady-state solution when no uptake occurs ($\omega_u = 0$); the sum of the first, the second (21b), and the third part (21c) gives the steady-rate solution in which the concentration is a linear function of time. The series parts (21d and e) account for the transient situation; these parts vanish in due course as time occurs in the exponent only with a negative coefficient.

Uniform replenishment in the soil cylinder

In principle, it should be possible to obtain a complete solution of (17) subject to (18)–(20) by employing the Laplace transformation. However, it turns out to be easier and more illuminating to solve the different parts of the total solution separately. One can expect the solution to have the following form (cf Eq. (21)):

$$c = p(r) + f(r)t + g(r) + h(r, t) \quad (22)$$

where the first function $p(r)$ represents the steady-state solution when uptake is zero, the sum of the first, the second $f(r)t$, and the third $g(r)$ function represents the steady-state solution, and the last function $h(r, t)$ accounts for transient terms in the solution.

Steady-State Solution

When uptake is zero, a steady-state situation will eventually develop in which transport by mass flow to the root is balanced by back diffusion from the root surface, then as stated above:

$$c = p(r) \quad (23)$$

Substitution of (23) in (16) leads to:

$$p'' + \frac{1 + \mu(\rho^2 - r^2)}{r} p' - 2\mu p = 0 \quad (24)$$

The solution in (24) can be found by defining new variables y and x , respectively, as (Kamke

1983, page 451, 2.215):

$$x = \frac{\mu r^2}{2} \tag{25}$$

$$y = px^{\mu\rho^2/2} \tag{26}$$

This transforms (24) into:

$$xy'' = (b - x)y' - by = 0 \tag{27}$$

where $b = 1 - \mu\rho^2/2$. The general solution of (27) is given by (Abramowitz and Stegun 1970):

$$y = A_0M(b, b, x) + B_0U(b, b, x) \tag{28}$$

where $M(b, b, x)$ and $U(b, b, x)$ are special cases of confluent hypergeometric (Kummer) functions, generally defined as (Abramowitz and Stegun 1970):

$$M(a, b, z) = \sum_{n=0}^{\infty} \frac{(a)_n z^n}{n!(b)_n}$$

where: $(a)_n = a(a + 1)(a + 2) \dots (a + n - 1)$, and:

$$U(a, b, z) = \frac{1}{\sin(\pi b)} \left[\frac{M(a, b, z)}{\Gamma(1 + a - b)\Gamma(b)} - z^{1-b} \frac{M(1 + a, 2 - b, z)}{\Gamma(a)\Gamma(2 - b)} \right]$$

It follows that:

$$M(b, b, x) = e^x,$$

$$U(b, b, x) = e^x \Gamma(1 - b, x) = e^x \Gamma(\mu\rho^2, x)$$

where $\Gamma(1 - b, x)$ is the incomplete gamma function with parameter $(1 - b)$ and argument x . The boundary conditions (18) and (19) transform into:

$$x = x_0 = \frac{\mu}{2}, \quad y - y' = 0 \tag{29}$$

$$x = x_1 = \frac{\mu\rho^2}{2}, \quad y - y' = 0 \tag{30}$$

Using Eq. (29), one finds that $B_0 = 0$. The constant A_0 cannot be evaluated from condition (30), since this condition holds for all values of A_0 . However, it can be found considering conservation of mass. For zero-uptake the total amount of nutrient in the soil cylinder should equal the initial amount. The total amount in dimensionless units is found as:

$$\int_1^{\rho} 2\pi\eta r c dr = \int_1^{\rho} 2\pi\eta r p dr = \frac{2\pi\eta A_0}{\mu} \int_{x_0}^{x_1} x^{b-1} e^x dx = \frac{2\pi\eta A_0 \{x_1^b M(b, b + 1, x_1) - x_0^b M(b, b + 1, x_0)\}}{b\mu}$$

The total initial amount is:

$$\pi\eta(\rho^2 - 1) = \frac{2\pi\eta}{\mu} (x_1 - x_0)$$

so that A_0 is found as

$$A_0 = \frac{b(x_1 - x_0)}{\{x_1^b M(b, b + 1, x_1) - x_0^b M(b, b + 1, x_0)\}} \tag{31}$$

The steady-state solution is thus:

$$p = A_0 e^x x^{-\mu\rho^2/2} \tag{32}$$

A_0 being given in (31).

Steady-Rate Solution

Because of the boundary conditions (constant and zero flux, respectively), in due course a steady-rate situation will develop in which the decrease of concentration will have become a function of distance only; the concentration can then be given as:

$$c = p(r) + f(r)t + g(r) \tag{33}$$

Substitution of (33) in (16), (17), and (18) yields, respectively:

$$Bf = \left[f'' + \frac{1 + \mu(\rho^2 - r^2)}{r} f' - 2\mu f \right] t \tag{34}$$

$$+ g'' + \frac{1 + \mu(\rho^2 - r^2)}{r} g' - 2\mu g$$

$$r = \rho, f't + g' = 0, \tag{35}$$

$$r = 1, [-f' + \mu(1 - \rho^2)f]t - g' + \mu(1 - \rho^2)g = \omega_u \tag{36}$$

As the left-hand side of (34) depends on r only and not on t , it follows that the expression within brackets [] on the right side has to vanish. The same applies to the coefficient f' of t in (35) and to the expression within brackets [] on the left side of (36). Thus, one obtains two systems of ordinary differential equations with boundary conditions, respectively:

$$f'' + \frac{1 + \mu(\rho^2 - r^2)}{r} f' - 2\mu f = 0 \tag{37}$$

$$r = 1, \quad -f' + \mu(1 - \rho^2)f = 0, \tag{38}$$

$$r = \rho, \quad f' = 0, \tag{39}$$

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and,

$$g'' + \frac{1 + \mu(\rho^2 - r^2)}{r} g' - 2\mu g = Bf, \quad (40)$$

$$r = \rho, \quad g' = 0, \quad (41)$$

$$r = 1, \quad -g' + \mu(1 - \rho^2)g = \omega_\mu \quad (42)$$

The solution for f is found similarly to that of p :

$$f = A_1 e^{\mu x} x^{-\mu^2/2} \quad (43)$$

The constant A_1 can be found by considering that the rate of decrease of the total nutrient in the soil cylinder equals the uptake rate, in dimensionless units:

$$\frac{d}{dt} \int_1^\rho r c dr = \int_1^\rho r \frac{\partial c}{\partial t} dr = \int_1^\rho r f dr = \frac{\omega_\mu}{B}$$

On evaluating the integral one eventually finds:

$$A_1 = \frac{\omega_\mu b \mu}{B \{x_1^b M(b, b+1, x_1) - x_0^b M(b, b+1, x_0)\}} \quad (44)$$

Applying the transformations (25) and (26), with g instead of p , to (40)-(42), and substituting (43), one obtains

$$xy'' + (b-x)y' - by = \frac{BA_1 e^x}{2\mu} \quad (45)$$

$$= x_1, \quad y - y' = 0, \quad (46)$$

$$x = x_0, \quad y - y' = \frac{x^{b-1} \omega_\mu}{\mu} \quad (47)$$

The solution of (45) is (Babister 1967):

$$y = A_2 M(b, b, x) + B_2 U(b, b, x)$$

$$W(b, -x) \frac{Be^x A_1}{2\mu} \quad (48)$$

$$= e^x \left\{ A_2 + B_2 \Gamma(1-b, x) - W(b, -x) \frac{BA_1}{2\mu} \right\}$$

where $W(b, x)$ is defined as:

$$W(b, -x) = -\frac{1}{b} \int M(1, b+1, -x) dx$$

$$= \sum_{n=1}^{\infty} \frac{(-1)^n x^n}{n(b)_n}$$

From (46) B_2 can be calculated as:

$$B_2 = x_1^b \frac{BA_1}{2b\mu} M(b, b+1, x_1) \quad (49)$$

As before, the constant A_2 has to be calculated by using a mass balance. The total amount of nutrient in the soil cylinder at any moment should equal the initial amount diminished by the total amount taken up:

$$\begin{aligned} \int_1^\rho 2rcdr &= \int_1^\rho 2r\{p(r) + f(r)t + g(r)\}dr \\ &= (\rho^2 - 1) + \frac{2\omega_\mu t}{B} \end{aligned}$$

Now: $\int_1^\rho 2rp(r)dr = \rho^2 - 1$, and: $\int_1^\rho 2rf(r)tdr = 2\omega_\mu t/B$, thus:

$$\begin{aligned} \int_1^\rho 2rg(r)dr &= \frac{2}{\mu} \int_{x_0}^{x_1} x^{b-1} y dx = \frac{2A_2}{\mu} \int_{x_0}^{x_1} x^{b-1} e^x dx \\ &+ \frac{2B_2}{\mu} \int_{x_0}^{x_1} x^{b-1} \Gamma(1-b, x) dx \\ &- \frac{BA_1}{\mu^2} \int_{x_0}^{x_1} e^x x^{b-1} W(b, -x) dx \\ \frac{2A_2}{\mu} I_1 + \frac{2B_2}{\mu} I_2 - \frac{A_1 B}{\mu^2} I_3 &= 0 \end{aligned}$$

By evaluating the integrals of (50), denoted by I_1, I_2 , and I_3 , one eventually finds:

$$I_1 = \frac{x_1^b M(b, b+1, x_1) - x_0^b M(b, b+1, x_0)}{b}, \quad (51)$$

$$\begin{aligned} I_2 &= \frac{\Gamma(1-b)}{b} \{x_1^b M(b, b+1, x_1) \\ &- x_0^b M(b, b+1, x_0)\} \\ &+ W(1-b, x_0) - W(1-b, x_1), \quad (52) \end{aligned}$$

$$I_3 = \frac{e^{x_1} x_1^b \Omega(b, x_1) - e^{x_0} x_0^b \Omega(b, x_0)}{b}$$

where:

$$\Omega(b, x) = \sum_{n=1}^{\infty} \frac{(-1)^n x^n}{(b+1)_n} \{ \psi(n) + 1 + \gamma \}$$

and $\psi(n)$ is the digamma function with argument n , and γ is Euler's constant. The constant A_2 can thus be given as:

$$A_2 = \frac{A_1 I_3 B}{2\mu I_1} - \frac{B_2 I_2}{I_1} \quad (54)$$

where A_1, B_2, I_1, I_2 , and I_3 are given, respectively, in (44), (49), and (51)-(53). The steady-rate

solution is thus obtained as:

$$c = e^x x^{-\nu\rho^{1/2}} \left\{ A_0 + A_1 t + A_2 + B_2 \Gamma(1-b, x) - W(b, -x) \frac{BA_1}{2\mu} \right\} \quad (55)$$

Transient Solution

The complete solution is given by (22), and substitution of (22) in (17) using (24), (37), and (40) yields:

$$B \frac{\partial h}{\partial t} = \frac{\partial^2 h}{\partial r^2} + \frac{1 + \mu(\rho^2 - r^2)}{r} \frac{\partial h}{\partial t} - 2\mu h \quad (56)$$

while the boundary conditions (17)-(18) and the initial condition (19) become:

$$\frac{\partial h}{\partial r} = 0, \quad (57)$$

$$r = 1 \quad - \frac{\partial h}{\partial r} + \mu(1 - \rho^2)h = 0, \quad (58)$$

$$t = 0, \quad -h = 1 - p - g \quad (59)$$

Equation (56) can be solved by the method of separation of variables (Churchill 1972), but the derivation of the solution will not be discussed here as our interest is focused on the steady-rate solution (55).

THE PERIOD OF UNCONSTRAINED UPTAKE

Replenishment from outside the soil cylinder

As long as the concentration at the root surface ($r = 1$) is greater than zero, transport through the soil is not limiting uptake, and uptake may be equal to plant demand. The period during which this is the case is called the period of unconstrained uptake T_u or t_u in dimensionless symbols. When the steady-rate solution (21a-21c) applies, it follows by setting $c = 0$ at the root surface where $r = 1$ such that:

$$t_u = t_{u,max} - BG(\rho, \nu) \quad (60)$$

where $t_{u,max}$ is the maximum period of unconstrained uptake, i.e., the total initial amount of nutrient divided by demand (De Willigen and Van Noordwijk 1987):

$$t_{u,max} = - \frac{(\rho^2 - 1)B}{2\omega_\mu} \quad (61)$$

and where

$$G(\rho, \nu) = \frac{1}{2(\nu + 1)} \left\{ \frac{1 - \rho^2}{2} + \frac{\rho^2(\rho^{2\nu} - 1)}{2\nu} + \frac{\rho^2(\rho^{2\nu} - 1)(\nu + 1)}{2\nu(\rho^{2\nu+2} - 1)} + \frac{(1 - \rho^{2\nu+4})(\nu + 1)}{(2\nu + 4)(\rho^{2\nu+2} - 1)} \right\}$$

Uniform replenishment in the soil cylinder

When the steady-rate solution (55) applies, an explicit expression for t_u can be derived by substituting $x = x_0$ and $c = 0$:

$$t_u = t_{u,max} - \frac{\{e^{x_1} x_1^b \Omega(b, x_1) - e^{x_0} x_0^b \Omega(b, x_0)\}}{2\mu \{x_1^b M(b, b + 1, x_1) - x_0^b M(b, b + 1, x_0)\}} + \frac{x_1^b}{2\mu} M(b, b + 1, x_1) \{\Gamma(1 - b) - \Gamma(1 - b, x_1)\} - b \frac{W(1 - b, x_1) - W(1 - b, x_0)}{x_1^b M(b, b + 1, x_1) - x_0^b M(b, b + 1, x_0)} + B \frac{W(b, -x_0)}{2\mu} \quad (62)$$

When transport is by diffusion alone ($\mu = 0$) t_u is given by:

$$t_u = T_{u,max} - \frac{B}{2} \left\{ \frac{1 - 3\rho^2}{4} + \frac{\rho^4 \ln(\rho)}{\rho^2 - 1} \right\} \quad (63)$$

as can be derived directly from (16)-(19) with $\mu = 0$ (De Willigen and Van Noordwijk 1987).

UNCONSTRAINED UPTAKE CAPACITY AND FRACTIONAL DEPLETION

The total amount taken up in the period t_u is the amount of nutrient available for unconstrained uptake, i.e., that amount of nutrient that can be taken up by the crop at the required rate. This amount is called the unconstrained uptake capacity. This can be expressed as a fraction of the available amount. As uptake is constant in time, it follows that this fractional depletion can be given as the ratio of t_u and $t_{u,max}$:

$$q_u = \frac{t_u}{t_{u,max}} \quad (64)$$

AVERAGE CONCENTRATION

The average concentration in the soil at the end of the period of unconstrained uptake sim-

ply reads:

$$c_u = 1 - \frac{t_u}{t_{u,max}} \quad (65)$$

where t_u is given by (60), (62), or (63).

RESULTS AND DISCUSSION

The assumption that water uptake of the root at any root density equals the demand of the plant leads to very high fluxes at the root surface at low root density; eventually as the root density approaches zero, it leads to infinite flux. In the calculations care has been taken that the water flux at the root surface did not exceed a maximum value, which was set at $0.43 \text{ ml cm}^{-2} \text{ day}^{-1}$ (De Willigen and Van Noordwijk 1987).

Figures 1-3 pertain to the situation where water is replenished uniformly over the soil cylinder. Figure 1 shows the steady-rate concentration profile (given by Eq. (55)) and its constituting components. The steady-state solution $p(r)$ is seen to be increasing toward the root surface because, when uptake is zero, back diffusion from the root just balances the mass flow toward the root. The function $f(r)$ is negative for all r , whereas $g(r)$ is increasing from negative values at low values of r to positive values at large r . Also, the concentration profile is shown when replenishment is from outside the soil cylinder (Eq. 21a-c); there is only a slight difference with the result of Eq. (55).

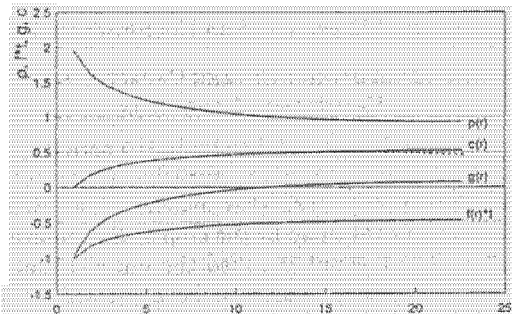


FIG. 1. Steady-rate profile of the concentration and the functions $p(r)$, $f(r)$, $g(r)$, and $h(r)$ (Eq. (22)). The interrupted line gives the steady-rate solution as calculated with Eq. (21a-c). Parameter values: root density $L_w = 1 \text{ cm cm}^{-2}$, adsorption constant $k_a = 10$, available amount of nutrient = 400 kg ha^{-1} , uptake rate $A = 2 \text{ kg ha}^{-1} \text{ d}^{-1}$, water content $\theta = 0.25 \text{ ml cm}^{-3}$, root length $H = 20 \text{ cm}$, transpiration $E = 1 \text{ cm d}^{-1}$, root radius $R_r = 0.925 \text{ cm}$, diffusion coefficient $D = 2.8 \cdot 10^{-2} \text{ cm}^2 \text{ d}^{-1}$.

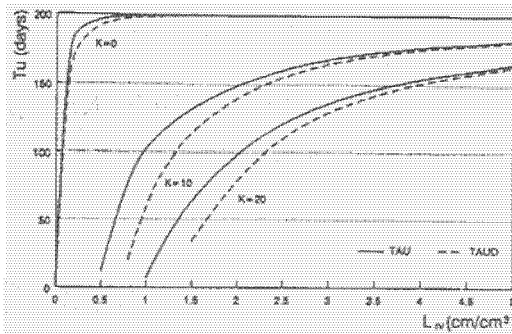


FIG. 2. Period of unconstrained uptake T_u in days as a function of root density L_w when transport is by diffusion and mass flow (solid lines, Eq. (62)) and by diffusion only (interrupted lines, Eq. (63)), respectively, for different values of the adsorption constant K_a . Other parameter values as in Fig. 1.

Figure 2 shows the period of unconstrained uptake T_u in days, as a function of root density, with evapotranspiration and adsorption constant as parameters. The increase of T_u caused by mass flow is more important the higher the adsorption constant (i.e., for a nutrient like phosphate; cf Robinson 1986), especially at low values of the root density. When adsorption is low (i.e., for a nutrient like nitrate), almost all of the nutrient can be taken up with the rate required by the crop when transport is by diffusion only, even at low root densities, at least for the value of the diffusion coefficient employed here.

Figure 3 displays T_u as a function of evapotranspiration, and it can be seen that its value extrapolates to the value where transport is by diffusion only, as it should.

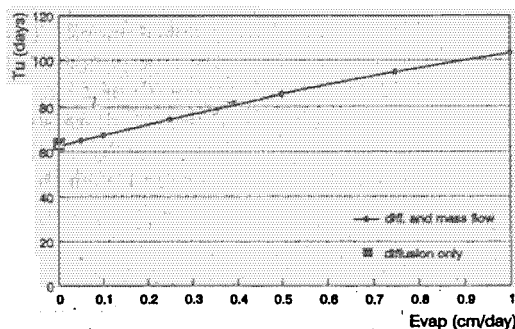


FIG. 3. Period of unconstrained uptake T_u in days as a function of transpiration E in cm d^{-1} (Eq. (62)). The point at $E = 0$ is calculated with Eq. (64). Other parameter values as in Fig. 1.

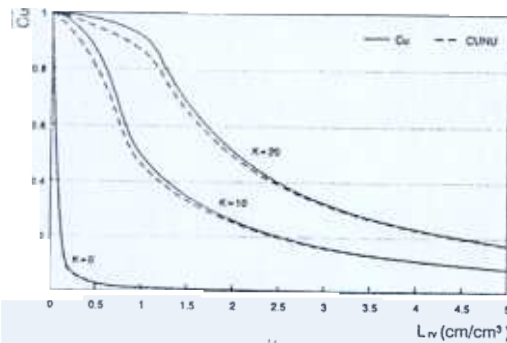


FIG. 4. Average concentration \bar{c}_w at the end of the period of unconstrained uptake for uniform replenishment of water (solid lines) and replenishment from outside the soil cylinder (interrupted lines).

Crop growth models treat the uptake of the root system in a macroscopic way, i.e., calculating uptake from the average concentration and root length density. When one can assume the distribution of the concentration around a root to follow the steady-rate distribution, at least when $T = T_u$, the average concentration at t_u is given by Eq. (65). As long as the average concentration in the soil exceeds c_u , uptake can proceed with the required rate. Figure 4 compares the average concentration in the soil cylinder at T_u when calculated for uniform replenishment (given by Eq. (62)) and for replenishment from outside the soil cylinder (given by Eq. (60)). Differences are slight, so it appears to be justified to use the transport equation (14) rather than Eq. (17) since it leads to simpler solutions.

At $T = T_u$, a considerable amount of available nutrients may be left in the soil, especially for low root densities, high demand, low soil water content (the diffusion coefficient strongly decrease with decreasing soil water content (Barraclough and Tinker 1981)), and/or high adsorption constant. Uptake of this amount will be described as a zero-sink process, and this will be the subject of the following paper.

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