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Modelling nutrient uptake: from single roots to complete root systems

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Introduction

Many models of water and nutrient balances have been successfully applied without explicit attention for the number, distribution and activity of roots. For fine tuning of fertilizer recommendations which is now required for environmental reasons, however, more precise descriptions of the uptake process may be needed and attention to quantitative root ecology is called for (van Noordwijk & de Willigen, 1986).

For modelling uptake by whole root systems, four levels of complexity can be distinguished (de Willigen & van Noordwijk, 1987).

- A. Models using measured root length density as a function of depth and data of root pattern on root maps as input, interpolating between experimental data.
- B. Models using descriptive curve-fits of rooting pattern in space and time under non-limiting soil conditions, e.g. negative exponential functions to describe root length density as a function of depth.
- C. Models based on 'functional equilibrium' concepts, relating overall root growth to the internal water and/or nutrient status of the plant. Distribution of new roots over various soil depths may follow either approach A or B.
- D. Models based on 'functional equilibrium' concepts, relating overall root growth to the internal water and/or nutrient status of the plant and relating root growth in any specific layer or zone of the soil to local conditions, such as: mechanical resistance as a function of soil water content, oxygen status as a function of internal and external aeration, nutrient concentrations, pH and aggregate structure to account for 'root pattern'.

Although models at level D may seem desirable, at the moment insufficient knowledge exists to formulate them and to determine all relevant parameters by independent measurements. As a first step, we will concentrate here on level A: evaluating the uptake potential of root systems as actually observed under field conditions.

For models at level A we will consider a root system as a number of typical single roots. In the simplest case only one single root is considered, but for more realistic models a frequency distribution is applied. The basis for such a division is a sensitivity analysis of parameters affecting the uptake potential of a single root. From transport models (de Willigen & van Noordwijk, 1987) we know that soil water content, root-soil contact and non-homogeneous root distribution have a considerable effect on the uptake rate of a single

root. A partitioning of a root system over representative single roots should be based on a classification taking these complications into account. We shall eventually deal here with non-homogeneous distribution of both water content and roots with depth. The procedure for integrating uptake of representative single roots, however, is equally valid for other types of division or for further subdivision.

Soil water plays a prominent role in determining the possible rate of uptake of nutrients. Firstly because uptake of water by the plant generates a flow of solutes towards the root. Secondly because even in the absence of any water uptake, the water content of the soil determines the possible rate of diffusion of the solutes. Therefore, we shall also pay attention to the interaction of water and nutrient uptake.

The objectives of this contribution are to present a mechanistic model for water and nutrient uptake that can be directly linked with field crop simulation models, and to list the assumptions made. It includes an attempt to validate the model by comparison with numerical solutions and with experimental observations.

Nutrient uptake and crop demand

A major problem in modelling nutrient uptake at the level of a whole root system is the degree of feedback or regulation of the uptake rate of an individual root by the nutrient status of the whole plant. Some authors have largely neglected such feedback (Nye & Tinker, 1977; Barber, 1984) and described the uptake by a whole root system as a simple summation of the uptake of single roots. In our approach complete regulation of uptake according to demand is assumed and two situations are distinguished:

- the sum of the current potential uptake rates of all roots is less than crop demand,
- the sum exceeds crop demand.

In the first situation we assume the plant to maximize its uptake rate, and our models are based on 'zero-sink' uptake by individual roots and are similar to models presented by other authors. In the latter situation we assume that crop demand determines current uptake by the root system as a whole.

The most general evidence for regulation of uptake is derived from the relative constancy of plant nutrient contents, under widely varying conditions. The difficulties of establishing reliable procedures for tissue analysis as indicators of nutrient supply, show that a plant is an efficient regulator. In experiments where the growth rate of the plant is modified, e.g. by variation in nitrogen supply, contents of other nutrients, such as potassium or phosphorus, in the crop usually do not change. Total potassium or phosphorus uptake by the crop thus depends on nitrogen supply, even when the size of the root system is unaffected. Models which relate nutrient uptake only to the size of the root system and the nutrient supply in the soil, necessarily fail to predict such effects (Barraclough, 1987). Results of recent plant physiological experiments suggest several mechanisms for such internal regulation, but also indicate that the regulation may involve a time-lag, especially relevant under rapidly changing conditions, and that regulation may be incomplete (Clarkson, 1985; de Willigen & van Noordwijk, 1987). Our assumption of complete and instantaneous regulation thus

represents a simplification which may be permitted when longer periods (e.g. weeks) are considered, but not when the short-term response (e.g. hours) is predicted. Crop demand for nutrients is defined here as the current rate of dry matter production multiplied by the nutrient content per unit dry weight typical for non-limiting conditions.

Nutrient uptake by a single root for 'zero-sink' conditions

For the single-root model we start by considering a vertical cylindrical root, situated within a cylinder of soil. Transport in the soil cylinder is by mass flow and diffusion. No transport will take place over its outer boundary. Uptake by the root is assumed to be independent of the concentration of the nutrient in the soil solution as long as this exceeds a certain limiting value C_{lim} ; when the concentration at the root surface drops below this value, uptake stops. The highest possible rate of uptake under any condition occurs when the concentration at the root surface is C_{lim} , i.e. when the root takes up all nutrient at the rate at which it arrives at the root surface. Consequently, this rate is the highest uptake rate transport through the soil will allow.

This system can be formulated in mathematical terms by a partial differential equation, describing transport by mass flow and diffusion in a hollow cylinder, together with initial and boundary conditions, the condition at the inner boundary (the root) being that of constant concentration and that at the outer boundary that of zero-flux. The transport equation in radial coordinates reads:

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

where K_a is the adsorption constant of the nutrient (ml cm^{-3}), θ is the water content (ml cm^{-3}), C is the concentration of the nutrient in the soil solution (mg ml^{-1}), T is time (d), D is the diffusion coefficient ($\text{cm}^2 \text{d}^{-1}$), R is the radial coordinate (cm), and V is the flux of water (cm d^{-1}). The diffusion coefficient D is calculated as (Barraclough & Tinker, 1981):

$$D = D_0 \theta f_i$$

where f_i is the impedance factor accounting for tortuosity of pores, dead-end pores, etc. which is a function of water content.

The boundary condition at the root surface is:

$$R = R_0, C = C_{lim} \quad (2a)$$

where R_0 is the radius of the root (cm). The boundary condition at the outer boundary is:

$$R = R_1, -2 \pi H R_1 D \frac{\partial C}{\partial R} + 2 \pi H R_1 V C = 0 \quad (2b)$$

where H is the length of the root (cm) and R_1 is the radius of the soil cylinder (cm). The relevant initial condition is that of constant concentration:

$$T = 0, C = C_i \quad (3)$$

where C_i is the initial concentration (mg mL^{-1}).

It is convenient to transform to dimensionless variables (Table 1), so that the transport equation reads:

$$\theta \beta \frac{\partial c}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} r \frac{\partial c}{\partial r} - \frac{2v}{r} \frac{\partial c}{\partial r} \quad (4)$$

and the boundary conditions:

$$r = 1, c = c_{\text{lim}} \quad (5a)$$

and

$$r = \rho, \frac{\partial c}{\partial r} + \frac{2v}{\rho} c = 0 \quad (5b)$$

The initial condition transforms into:

$$t = 0, c = 1 \quad (6)$$

The analytical solution for the concentration is now given by (de Willigen & van Noordwijk, in preparation):

$$c = -2 \pi c_{\text{lim}} \sum_{n=0}^{\infty} \frac{2vJ_v^2(\alpha_n) - \alpha \rho^{v+1} J_v(\alpha_n) J_{v+1}(\alpha_n) r^v C_v(r\alpha_n)}{J_v^2(\alpha_n) - J_{v+1}^2(\rho\alpha_n)} \frac{r^v C_v(r\alpha_n)}{\rho^{v+1} \alpha_n} e^{\frac{-\alpha_n^2 t}{\theta \beta}} \quad (7)$$

where α_n is the n -th zero of:

$$Y_v(\alpha) J_{v+1}(\rho\alpha) - Y_{v+1}(\rho\alpha) J_v(\alpha) = 0$$

where $J_v(\alpha)$ and $Y_v(\alpha)$ denote Bessel functions of the first and second kind, respectively, with order v and argument α . The uptake rate can be derived as:

$$\omega_r = \left(\frac{\partial c}{\partial r} \right)_{r=1} = -2 c_{\text{lim}} \sum_{n=0}^{\infty} \frac{2vJ_v(\alpha) J_{v+1}(\rho\alpha) - \alpha \rho^{v+1} J_{v+1}^2(\rho\alpha)}{\alpha (J_v^2(\alpha) - J_{v+1}^2(\rho\alpha))} e^{\frac{-\alpha_n^2 t}{\theta \beta}} \quad (8)$$

Now it can be shown (de Willigen & van Noordwijk, 1987) that the complicated expression for uptake Equation 8 can very well be approximated by a much simpler equation, relating

uptake to the average concentration in the soil cylinder:

$$\omega_t = \frac{(\rho^2 - 1)}{2G(\rho, \nu)} (\bar{c} - c_{lim}) \quad (9)$$

with

$$G(\rho, \nu) = \frac{1}{2(\nu+1)} \left(\frac{1-\rho^2}{2} + \frac{\rho^2(\rho^{2\nu}-1)}{2\nu} + \frac{\rho^2(\rho^{2\nu}-1)(\nu+1)}{2\nu(\rho^{2\nu+2}-1)} + \frac{(1-\rho^{2\nu+4})(\nu+1)}{(2\nu+4)(\rho^{2\nu+2}-1)} \right) \quad (10)$$

and \bar{c} is the average dimensionless concentration in the soil cylinder.

Figure 1 shows cumulative uptake calculated from the exact solution Equation 8 and from its approximation Equation 9, for different conditions.

Table 1. List of symbols used in text.

Symbols	Name	Dimension	Dimensionless symbol
R_0	root radius	cm	
D	diffusion coefficient	cm ² d ⁻¹	
T	time	day	$t = DT/R_0^2$
R	radial coordinate	cm	$r = R/R_0$
R_1	radius soil cylinder	cm	$\rho = R_1/R_0$
H	root length	cm	$\eta = H/R_0$
A	uptake rate	mg cm ⁻² d ⁻¹	$\omega = -\rho^2 \theta \beta / (2\phi \eta)$
C_i	initial nutrient concentration	mg ml ⁻¹	
C	nutrient concentration	mg ml ⁻¹	$c = C/C_i$
θ_i	initial water content	ml cm ⁻³	
θ	water content	ml cm ⁻³	
K_a	adsorption constant	ml cm ⁻³	
$\theta\beta$	buffer capacity	ml cm ⁻³	$\beta = (K_a + \theta)/\theta$
U_1	flow of water over the root surface	cm d ⁻¹	
U_2	flow of water from bulk soil to root surface	cm d ⁻¹	
E_{act}	actual transpiration rate	cm d ⁻¹	
E_{pot}	potential transpiration rate	cm d ⁻¹	-
V	flux of water	cm d ⁻¹	$2\nu = RV/D$
P	pressure head	cm	
D_w	diffusivity	cm ² d ⁻¹	
K	hydraulic conductivity	cm ² d ⁻¹	
Φ	matrix flux potential	cm ² d ⁻¹	
Φ_{rs}	matrix flux potential at root surface	cm ² d ⁻¹	

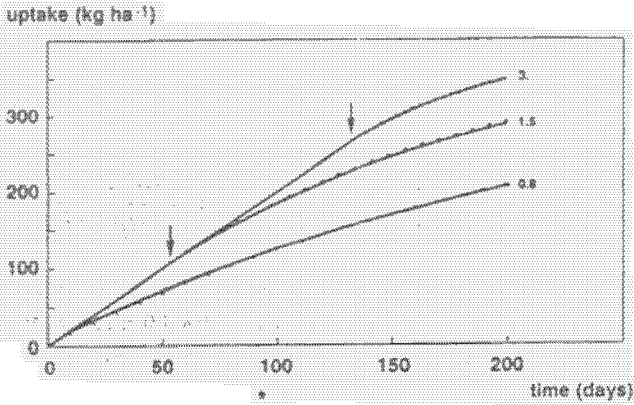


Figure 1. Cumulative uptake calculated with the exact solution Equation 8 and the steady-rate approximation. Parameters: available amount 400 kg ha^{-1} , required uptake rate $2 \text{ kg ha}^{-1} \text{ d}^{-1}$, root length 20 cm , root radius 0.02 cm , transpiration rate 0.5 cm d^{-1} , diffusion coefficient $0.028 \text{ cm}^2 \text{ d}^{-1}$, adsorption constant 20 ml cm^{-3} , limiting concentration $C_{\text{lim}} = 0$. Constant uptake rate followed by 'zero-sink' uptake (beginning indicated by arrow). The lines give the exact solution the points the steady-rate approximation. The figures near the curves denote the root length density in cm cm^{-3} . For root density 0.8 cm cm^{-3} 'zero-sink' uptake from time = 0.

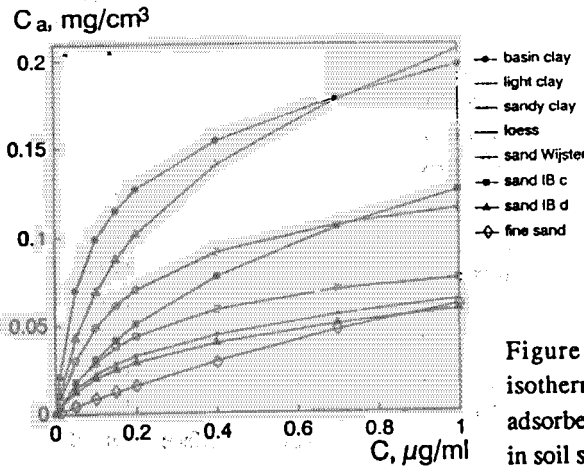


Figure 2. Phosphorus adsorption isotherms for eight Dutch soils. C_a is adsorbed phosphorus, C is concentration in soil solution.

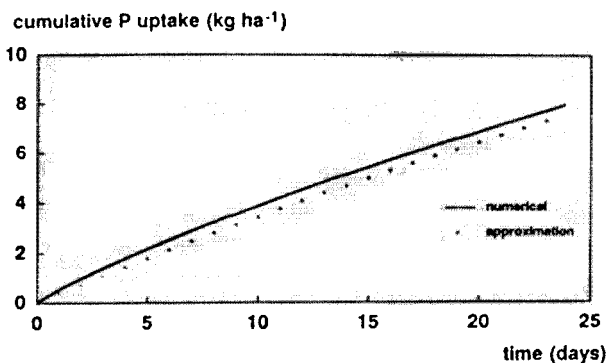


Figure 3. Cumulative phosphorus uptake calculated with numerical model and with the approximation. Parameters pertain to potato as given by van Noordwijk et al. (1990): root density 1.5 cm cm^{-3} , root radius 0.025 , root length 25 cm , $C_{lim} 3.2 \cdot 10^{-5} \text{ mg ml}^{-1}$. Transpiration rate 0.5 cm d^{-1} .

The above derivations pertain to nutrients with a linear adsorption isotherm such as nitrate, ammonium and to a certain degree potassium. For nutrients with a strongly non-linear adsorption isotherm, e.g. phosphorus (Figure 2), the governing transport equation is non-linear and no analytical solution exists. To obtain a complete solution one has to resort to numerical methods. It nevertheless appears that the uptake can be approximated by Equation 9 as well, as illustrated in Figure 3.

Nutrient uptake by a root system

One class of representative roots For a root system consisting of uniformly distributed roots confined to a single layer of uniform initial nutrient concentration, the potential uptake rate per unit soil surface simply is the product of the root length density and the potential uptake rate of a single root as given by Equation 8 and approximated by Equation 9. In absolute units:

$$A_p = L_{rv} 2\pi HR_0 D \left(\frac{\partial C}{\partial R} \right)_{R=R_0} = L_{rv} 2\pi H D C_i \left(\frac{\partial c}{\partial r} \right)_{r=1} = 2\pi H D L_{rv} (\bar{C} - C_{lim}) \frac{(\rho^2 - 1)}{2G(\rho, \nu)} \quad (11)$$

where A_p is potential uptake rate per unit surface ($\text{mg cm}^{-2} \text{ d}^{-1}$), and L_{rv} root length density (cm cm^{-3}).

If the required uptake rate is given by A_r ($\text{mg cm}^{-2} \text{ d}^{-1}$) it is assumed that the actual uptake rate A_a equals the required uptake rate as long as this is below the potential uptake

rate, otherwise it equals the potential uptake rate:

$$A_d = A_r \quad \text{for } A_r \leq A_p \\ A_p \quad \text{for } A_r > A_p$$

If it is assumed that the relevant parameters, e.g. root length density, required uptake rate, water content, and transpiration, are constant over a certain period, say T_s , Equation 11 offers the possibility to estimate the total supply of a nutrient required to ensure its adequate uptake. At the end of the period, the average concentration should at least be such that A_p equals A_r , or:

$$\bar{C} = C_{\text{lim}} + \frac{2A_r G(\rho, v)}{2\pi HDL_{rv}(\rho^2 - 1)} \quad (12)$$

The total amount present at the end of the uptake period can be calculated from its average concentration and to compute the total necessary supply, this has to be augmented with the total amount taken up in the period T_s , which simply is $A_r T_s$.

Non-uniformly distributed roots When different horizons in the root zone are distinguished, each with its own root density and nutrient concentration, the situation is more complicated. It is conceivable, as indeed is often found, that roots in favourable positions can compensate for roots in less favourable positions by increasing their uptake rates (de Jager, 1985). It is therefore assumed that the uptake rate of roots in a certain layer depends on the uptake potential of roots in other layers.

Uptake is now calculated iteratively. First (step 1) the nutrient demand is divided by the total root length to obtain the required uptake per unit root length. Multiplying this by the root length in a given layer yields the required uptake from that layer. If the potential uptake rate exceeds the required uptake rate, actual uptake from this layer equals the required uptake. In the opposite situation it is equal to the potential uptake rate. For convenience, those layers where actual uptake equals potential uptake, are tagged as layers of category 1.

Total uptake by the root system is the sum of the uptake rates from the individual layers. If the uptake in each layer can proceed at the required rate, total uptake equals nutrient demand and no iteration is required. If total uptake is less than nutrient demand, it is checked whether uptake from those layers where the concentration was sufficiently high to meet the original demand (for that particular layer), can be increased to increase total uptake, possibly enough to meet total demand.

This is achieved as follows. In step 2, first the difference between demand and total uptake, as calculated in step 1, is divided by the total root length in those layers (category 2) that were able to satisfy the required uptake rate of step 1. This yields an additional demand. The required uptake rate for layers of category 2, in step 2, is set equal to the required uptake rate of step 1, augmented with the additional demand. Next it is examined whether the potential uptake rate still exceeds the new value of the required uptake rate. If not, the

uptake rate from this layer is set equal to the potential uptake rate. If all layers of category 2 can satisfy the required uptake in step 2, total uptake equals demand and the iteration ends. If none of the layers of category 2 can satisfy the required uptake in step 2, i.e. if in all layers of category 1 and 2 'zero-sink' uptake occurs, the iteration also ends. If only part of the layers of category 2 can satisfy the required uptake in step 2, iteration proceeds to step 3, etc.

This calculation procedure implies that roots, growing under favourable conditions, will compensate as much as possible for roots growing under less favourable conditions. It is thus assumed that information about the necessary behaviour with respect to uptake, is instantaneously available throughout the complete root system.

This procedure can also be applied when roots within a horizon are not distributed uniformly. The layer is then divided into a number of compartments each with an uniform root distribution.

Modelling uptake of water

Uptake by a single root

For the single-root model we again start by considering a vertical cylindrical root, situated within a cylinder of soil. Over the outer boundary of the cylinder no transport takes place. At the inner boundary (the root surface) the water content is assumed to be constant. The partial differential equation describing transport of water in the soil (Richards equation), is strongly nonlinear, which makes finding analytical solutions generally very difficult, hence we had to resort to numerical techniques (fully implicit finite difference scheme Patankar (1980)).

As shown earlier (de Willigen & van Noordwijk, 1987) the numerical solution may be approximated by a so-called steady-rate approximation in terms of the matric flux potential (cf. Raats, 1970), which for our purpose is defined as:

$$\Phi = \int_{\theta}^{\theta_{sat}} D_w d\theta = \int_P^0 K dP \quad (13)$$

where K is the hydraulic conductivity in cm d^{-1} , P is the pressure head in cm water , D_w is the diffusivity in $\text{cm}^2 \text{d}^{-1}$, and θ the water content in ml cm^{-3} . The steady-rate solution in terms of the matric flux potential is:

$$\Phi = \Phi_{rs} + \frac{\rho^2}{2\eta} U_2 R_0 \left(\frac{r^2 - 1}{2(\rho^2 - 1)} - \frac{\rho^2 \ln r}{\rho^2 - 1} \right) \quad (14)$$

where Φ_{rs} is the matric flux potential at the root surface, and U_2 the flow of water towards the root. From Equation 14 an expression can be derived giving U_2 as a function of the average matric flux potential in the soil:

$$U_2 = 2\pi H L_{rv} (\Phi_{rs} - \Phi) \frac{\rho^2 - 1}{2G(\rho, 0)} \quad (15)$$

Note the similarity of Equations 15 and 11. The function $G(\rho, 0)$ can be derived from Equation 10 by taking the limit as $v \rightarrow 0$:

$$G(\rho, 0) = \frac{1}{2} \left(\frac{1 - 3\rho^2}{4^{1/3}} + \frac{\rho^4 \ln \rho}{\rho^2 - 1} \right) \quad (16)$$

Figure 4 shows cumulative water transport to the root for constant uptake (0.5 cm d^{-1}) until the pressure head at the root surface P_{rs} drops to 0.5 MPa, after which it is kept constant at that value, calculated with the numerical model and with the steady-rate approximation (Equation 15). The approximation is shown to be quite satisfactory.

Uptake by a root system

We start with considering a single layer of soil containing vertical and uniformly distributed roots. The flow of water over the root surface is supposed to be linearly related to the difference between plant water potential and pressure head of the soil water at the root surface (de Willigen & van Noordwijk, 1987):

$$F_w = k_1 (P_{rs} - P_p) + k_2 \quad (17)$$

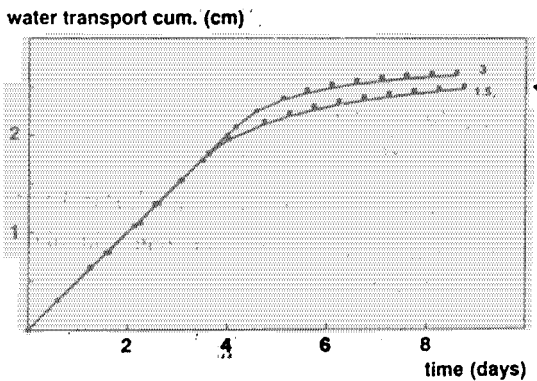


Figure 4. Cumulative transpiration calculated with the numerical model (solid lines) and with the approximation (symbols). Transpiration was set constant at 0.5 cm d^{-1} , until the pressure head at the root surface reached 5000 cm, and subsequently is kept constant at that value. The numbers near the curves denote the root length density in cm cm^{-3} .

where F_w is the flux of water in $\text{cm}^3 \text{ cm}^{-1} \text{ root d}^{-1}$, P_{rs} is the pressure head at the root surface in cm, P_p is the plant water potential in cm, and k_1 in cm d^{-1} and k_2 in $\text{cm}^3 \text{ cm}^{-1} \text{ root d}^{-1}$ are coefficients related to root conductivity.

If the thickness of the soil layer is Δx cm and the root length density L_{rv} cm cm^{-3} , the uptake U_1 in cm^3 water per cm^2 soil surface per day is given by:

$$U_1 = L_{rv} \Delta x F_w = q (P_{rs} - P_p) + v$$

where $q = L_{rv} \Delta x k_1$, and $v = L_{rv} \Delta x k_2$.

We assume that no water can accumulate at the root surface, so that U_1 equals the supply of water to the root. The flow from the bulk soil in the layer with matric flux potential Φ towards the root surface, where the matric flux potential is Φ_{rs} is given by (cf. Equation 13):

$$U_2 = s(\Phi_{rs} - \Phi) \tag{19}$$

where

$$s = \pi \Delta x L_{rv} (\rho^2 - 1) / G(\rho, 0)$$

whereas a functional relationship exists between Φ and P (see definition of Φ in (Equation 13)).

If the required uptake is given as E_{act} (the transpiration rate in cm d^{-1} the right hand side of Equation 19 should equal E_{act} , and the resulting equation can simply be solved for Φ_{rs} . Using the inverse of Equation 13, P_{rs} is calculated. Finally, because

$$U_1 = U_2 = E_{act},$$

the plant water potential can be computed from Equation 18 as:

$$P_p = P_{rs} - (E_{act} - v) / q$$

The situation is in fact more complicated, because the actual transpiration rate is a function of plant water potential:

$$E_{act} = f(P_p) E_{pot} \tag{21}$$

where $f(P_p)$ is a factor by which the potential transpiration E_{pot} has to be reduced. As $f(P_p)$ is a nonlinear function of P_p , E_{act} and P_{rs} have to be found by iteration.

When the root system is distributed over n different layers, but roots are assumed to be

distributed uniformly within each layer, for each layer Equations like 18 and 19 can be formulated. Equating these equations, one finds for the i -th layer:

$$q_i (P_{rs,i} - P_p) + v_i = s_i (\Phi_{rs,i} - \Phi_i) \quad (22)$$

It is assumed that the plant water potential P_p is identical throughout the root system. In total, there are n equations of the form of Equation 16, and $n+1$ unknowns i.e. $P_{rs,1} - P_{rs,n}$ (where again Equation 8 can be used to calculate Φ from P or vice-versa) and P_p . When the uptake rate E_{act} is known, an additional equation states that the sum of the flows over the root surface of all layers of the root zone equals E_{act} :

$$\sum_{i=1}^n q_i (P_{rs,i} - P_p) + v_i = E_{act} \quad (23)$$

When one takes into account the relation between plant water potential and uptake rate, Equation 21 has to be used. Because of the nonlinearity of Equations 13 and 21, again the solution has to be found by iteration.

Results

Required phosphorus level in the soil for different crops

The phosphorus fertilizer recommendation for arable crops in the Netherlands is based on the so-called Pw-value of the plow layer (the upper 20 - 25 cm of the soil profile). This value gives the amount of phosphorus, expressed in mg P_2O_5 per liter soil, soluble in water at an extraction ratio of 60 volumes of water to 1 volume of soil (van der Paauw, 1971). It was shown by de Willigen & van Noordwijk (1978) and van Noordwijk et al. (1990) that the Pw-value can be calculated with reasonable accuracy on the basis of 24 h P-adsorption isotherms, and the total amount of labile P, as measured by anion exchange resins or iron-hydroxide-impregnated filter paper.

Van Noordwijk et al. (1990) used Equation 12 to calculate the minimum required phosphorus supply of the soil for maximum growth of a number of crops and two groups of soils and compared these with experimentally established values for required phosphorus supply. For each crop, representative values for daily P demand and root length density were used. Figure 5 presents the results. Although there is no complete agreement between theoretical and experimental results, the values are strongly correlated. This at least indicates that the P level in the soil necessary to meet the phosphorus requirements of crops can be estimated with Equation 12.

Nitrogen uptake by a maize crop in the humid tropics

De Willigen & van Noordwijk (1989) applied the procedure explained in section 'Non-uniformly distributed roots' to describe nitrogen uptake of a maize crop growing under humid tropical conditions. Calculations were based on measured root length densities in

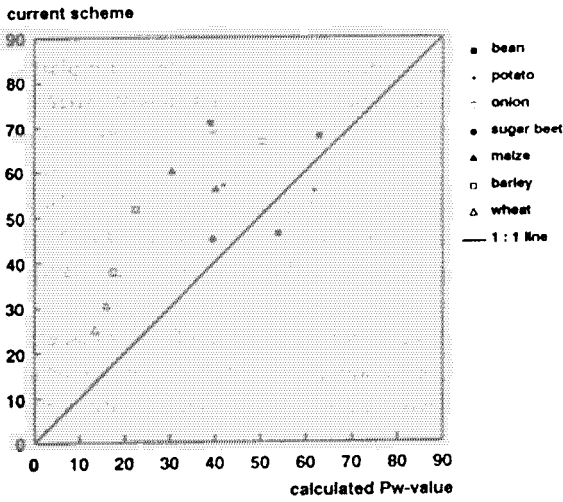


Figure 5. Comparison of the required Pw-value calculated with Equation 12 and required Pw-value as estimated from results of field experiments.

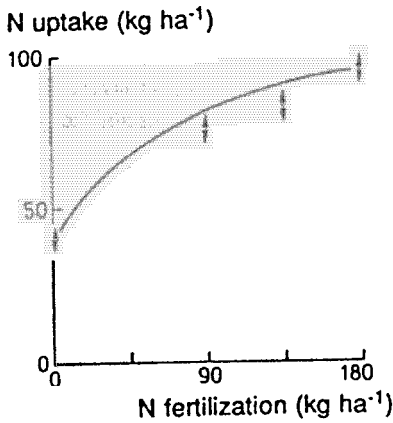


Figure 6. Nitrogen uptake as a function of N fertilization in experiments at Onne (S.E. Nigeria). Calculated uptake (line) is compared with experimental results; the vertical lines indicate the range of the experimental results.

various soil layers. Heterogeneous root distribution in a horizontal plane was taken into account. Daily crop nitrogen demand was calculated with a submodel for crop growth and required crop nitrogen content. Figure 6 shows some results. Using the model, subsequently effects of different root length distributions and patterns of water infiltration were explored. This led to the design of a series of experiments in which different ways to increase N-uptake efficiency suggested by model calculations are tested.

Water uptake by maize plants as a function of root length distribution and soil water content

The model described in section 'Uptake by a root system' has been tested with data of Sharp & Davies (1985), from an experiment with maize plants. Eighty plants were grown individually on cylindrical tubes filled with compost. After a preliminary growth period, half of the plants were watered daily, where care was taken to replenish the water lost by transpiration, whereas the other half of the plants were not watered at all. Every three days some tubes were harvested and soil water content, root length distribution, total dry matter and its distribution were measured, as well as, prior to harvest, leaf water potential. Soil water depletion rates were calculated from the changes in soil water content between successive sampling dates.

No data on diffusivity as a function of water content were given, and the information about the moisture retention curve was rather incomplete. Nevertheless, the data were used to examine the performance of the model. To this end, the model was run with data on hydraulic properties of a sandy loam (Lov16b, Boekhold, 1987). Results are shown in Figures 7 and 8.

Figure 7 shows the distribution of water uptake with depth for the well-watered plants, 15 days after the start of the experiment. Here uptake is more or less proportional to root length density as the dominant resistance in the pathway bulk soil - rhizosphere - root xylem is found at the root wall.

This is different for the dry treatment (Figure 8): here the highest uptake does not take place in the layers with the highest root density but in the lower layers where the moisture content is considerably higher than in the upper layers. The model predicts more or less the same distribution of water uptake as had been established experimentally.

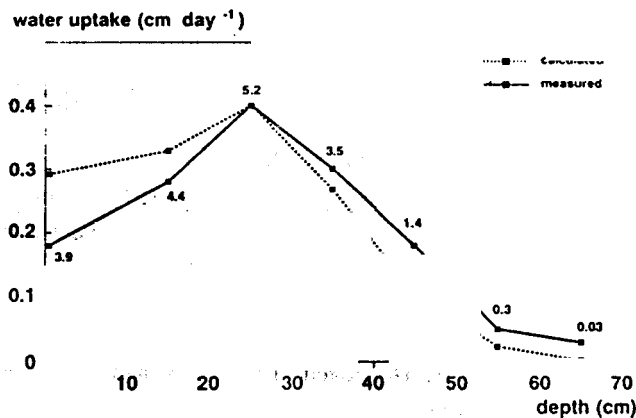


Figure 7. Measured and calculated depth distribution of water uptake rate per depth interval of 10 cm, for a maize plant in a soil kept at field capacity. The numbers in the figure refer to measured values of root length density (cm cm^{-3}). Source: Sharp & Davies (1985). For the calculations a root conductivity (k_1) of $10^{-5} \text{ cm d}^{-1}$ was used.

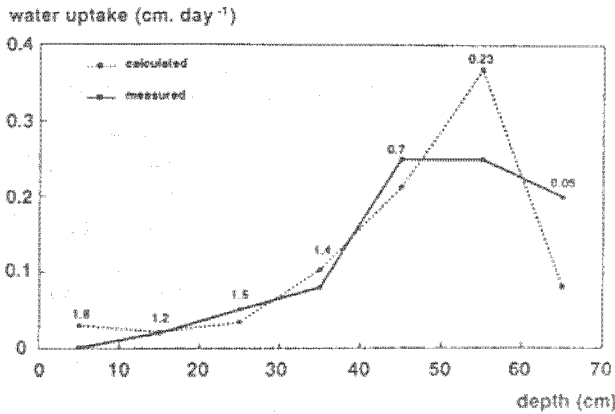


Figure 8. As Figure 7, but in a soil not watered for 15 days.

Interaction between water and nutrient uptake

By using a combination of the models for uptake of water and uptake of nutrients, the interaction between water and nutrient uptake can be examined. As an example a soil profile of 90 cm is considered, consisting of three equal layers with root densities of 1.5, 0.7 and 0.2 cm cm^{-3} , respectively, corresponding to the depth distribution of root density of potato as measured by Vos & Groenwold (1986). The nutrient to be taken up is nitrate.

The first example (Table 2) pertains to a situation in which the upper layer is dry, having a water content corresponding to a pressure head of 2000 cm, whereas the lower layers are moist (pressure head 200 and 100 cm, respectively). In that situation water uptake in the upper layer is negligible, but this can be compensated by uptake by the roots from lower layers. One can expect that the nitrate is concentrated in the upper layer, because it is applied at the surface and its downward movement during the growing season will be limited due to the surplus of evapotranspiration over precipitation. In such conditions, the uptake of nitrogen in the upper layer is seriously hampered despite the high concentration of nitrate there (Table 3). The possibilities for transport in the lower layers are much better, but here the nitrogen concentrations are low.

Table 2. Distribution of water uptake with depth for a soil profile of 90 cm, as a function of root length density and pressure head distribution. Dry upper layer.

Depth (cm)	Root density (cm cm^{-3})	Pressure head (cm)	Water uptake (cm d^{-1})
0-30	1.5	2000	0.0032
30-60	0.7	200	0.379
60-90	0.2	100	0.118

Plant water potential: 2000 cm; Transpiration: 0.5 cm d^{-1}

Table 3. Distribution of nitrogen uptake with depth and total nitrogen uptake for the soil water situation of Table 2. Nitrate mainly concentrated in upper layer.

Depth (cm)	Root density (cm cm ⁻³)	Diffusion coefficient (cm ² d ⁻¹)	N uptake (kg ha ⁻¹ d ⁻¹)	N content (kg ha ⁻¹)
0-30	1.5	1.32•10 ⁻³	2.08	50
30-60	0.7	9.98•10 ⁻²	0.50	1
60-90	0.2	0.151	0.15	1

Nitrogen demand: 6 kg ha⁻¹ d⁻¹

Nitrogen uptake: 2.7 kg ha⁻¹ d⁻¹

Table 4. Distribution of water uptake with depth for a soil profile of 90 cm, as a function of root length density and pressure head distribution. Moist upper layer.

Depth (cm)	Root density (cm cm ⁻³)	Pressure head (cm)	Water uptake (cm d ⁻¹)
0-30	1.5	200	0.307
30-60	0.7	200	0.143
60-90	0.2	100	0.050

Plant water potential: 2000 cm

Transpiration: 0.5 cm d⁻¹

Table 5. Distribution of nitrogen uptake with depth and total nitrogen uptake for the soil water situation of Table 4. Nitrate mainly concentrated in upper layer.

Depth (cm)	Root density (cm cm ⁻³)	Diffusion coefficient (cm ² d ⁻¹)	N uptake (kg ha ⁻¹ d ⁻¹)	N content (kg ha ⁻¹)
0-30	1.5	9.98•10 ⁻²	5.37	50
30-60	0.7	9.98•10 ⁻²	0.49	1
60-90	0.2	0.151	0.15	1

Nitrogen demand: 6 kg ha⁻¹ d⁻¹;

Nitrogen uptake: 6 kg ha⁻¹ d⁻¹

Table 6. Distribution of nitrogen uptake with depth and total nitrogen uptake for the soil water situation of Table 3, but in absence of transpiration. Nitrate mainly concentrated in upper layer.

Depth	Root density (cm cm ⁻³)	Diffusion coefficient (cm ² d ⁻¹)	N uptake (kg ha ⁻¹ d ⁻¹)	N content (kg ha ⁻¹)
0-30	1.5	9.98•10 ⁻²	5.37	50
30-60	0.7	9.98•10 ⁻²	0.49	1
60-90	0.2	0.151	0.15	

Nitrogen demand: 6 kg ha⁻¹ d⁻¹;

Nitrogen uptake: 6 kg ha⁻¹ d⁻¹

Table 7. Distribution of nitrogen uptake with depth and total nitrogen uptake for the soil water situation of Table 6. Nitrate mainly concentrated in second layer.

Depth	Root density (cm cm ⁻³)	Diffusion coefficient (cm ² d ⁻¹)	N uptake (kg ha ⁻¹ d ⁻¹)	N content (kg ha ⁻¹)
0-30	1.5	1.32•10 ⁻³	0.042	
30-60	0.7	9.98•10 ⁻²	5.81	50
60-90	0.2	0.151	0.15	

Nitrogen demand: 6 kg ha⁻¹ d⁻¹;

Nitrogen uptake: 6 kg ha⁻¹ d⁻¹

Table 8. Herbage yield and nitrogen recovery of a grass sward with surface application and injection of nitrogen at 40 cm depth. Source: Garwood & Williams (1967).

	Herbage yield (dm t ha ⁻¹)	N recovery (%)
Surface application	3.1	37
Injected at 40 cm	4.5	75

When the upper layer has the same pressure head as the second layer (200 cm), most water is taken up in the upper layer (Table 4); consequently, here also most nitrate is taken up and the nitrogen demand can easily be met (Table 5). This would even have been the case when transport would have been by diffusion only (Table 6).

Table 7, finally, pertains to a situation with the same distribution of water content and thus water uptake as shown in Table 4, but with the majority of the nitrate concentrated in the second layer. Now also the nitrogen demand can be met.

The last example qualitatively agrees with experimental results of Garwood & Williams (1967), who in a dry period applied nitrogen to the surface of a grass sward and at a depth of 40 cm. Table 8 summarizes their results. Despite the presumably lower root length density at a depth of 40 cm, recovery was much higher for nitrogen injected at this depth than for surface applied nitrogen.

Conclusions

The examples show that situations may occur (e.g. those considered in Tables 2 and 3) where, in order to obtain optimal crop growth, irrigation has to be applied not because of deficiency of water *per se*, but to ensure sufficient transport possibilities for nutrients in the soil. When models are used to evaluate the effect of e.g. improved drainage resulting in lowering of the groundwater table one has to take care to take into account effects on availability of nutrients.

It appears that the uptake of water and nutrients can be described fairly well by the proposed model. The approach is based on the calculation of water and solute transport from the bulk soil to the root surface under given distributions of water, nutrients and active roots over the soil profile. It is expected that the model can help to evaluate uptake of water and nutrients under the complex field conditions occurring in rainfed agriculture.

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