II-7: ·Model for interactions between water and nutrient uptake

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1 Introduction

Many models of water and nutrient balance have been successfully applied without explicit attention to the number, distribution and activity of roots. In the finer tuning of soil fertility recommendations, which is now required for environmental reasons, more precise descriptions of the uptake process and attention to quantitative root ecology are 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 measurements of root length density as a function of depth, and data of rooting pattern and root maps with interpolation between experimental data.
B. Models using descriptive curve-fits to root growth 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 nutrient status in 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 nutrient status in 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, aeration status as a function of internal and external aeration, local nutrient concentrations, local pH and local 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 found 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 used. The basis for such a division is found in 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 division 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.

Water in soil 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 flow the water content of the soil determines the possible rate of diffusion of the solutes. Therefore, we shall also consider the interaction of water and nutrient uptake.

2 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. Other 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 a complete regulation of uptake according to demand is assumed and two situations are distinguished:
- the sum of the possible current uptake rates of all roots is less than crop demand;
- the sum of the possible current uptake rates exceeds crop demand.

In the first situation we assume the plant maximizes 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 second 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 found in the relative constancy of plant nutrient concentration, i.e. the total amount of nutrient per unit dry weight in the plant, under widely varying conditions (Greenwood & Draycott, this book). 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, concentrations of other nutrients, such as potassium or phosphate, in the crop usually do not change. Total potassium or phosphate 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 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 certain time-lag, particularly noticeable 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

appropriate over longer periods (e.g. weeks) but not when short-term responses (e.g. hours) are considered. 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 well-fed plants.

2.1 Nutrient uptake by a single root for zero-sink condition

For the single-root model we start by considering a vertical cylindrical root. The root is situated within a cylinder of soil. Over the outer boundary of this cylinder no transport will take place. Transport in the soil cylinder is by mass flow and diffusion. Uptake of 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 fastest 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 determined by the rate of transport through the soil. The term zero-sink condition will be used for such a situation, though strictly speaking this term only applies when C_{lim} is zero.

   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 at the outer boundary that of zero-flux. The transport equation in radial coordinates is

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

where:
K_a = adsorption constant of the nutrient
θ = water content (cm^3 cm^{-3})
C = concentration of the nutrient in the soil solution (mg ml^{-1})
T = time (day)
D = diffusion coefficient (cm^2 day^{-1})
R = radial coordinate (cm)
V = flux of water (cm day^{-1})

The diffusion coefficient D is calculated as (Barraclough & Tinker, 1981)

$$D = D_0 \theta f_1 \qquad (2)$$

where:
f_1 = impedance factor accounting for tortuosity of pores, dead-end pores etc.
D_0 = diffusion coefficient in water

The impedance factor is a function of water content. The boundary condition at the root surface is,

$$R = R_0, \ C = C_{lim} \tag{3}$$

where:
R_0 = the radius of the root (cm).

The boundary condition at the outer boundary is,

$$R = R_1, \ -2\pi HR_1 D \frac{\partial C}{\partial R} + 2\pi HR_1 VC = 0 \tag{4}$$

where:
H = length of the root (cm)
R_1 = radius of the soil cylinder (cm)

The relevant initial condition is that of constant concentration,

$$T = 0, \ C = C_i \tag{5}$$

where:
C_i = initial concentration (mg ml^{-1})

It is convenient to employ dimensionless symbols (Table 1); the transport equation and the two boundary equations read,

$$\theta\beta \frac{\partial c}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r} \ r \ \frac{\partial c}{\partial r} - \frac{2v}{r}\frac{\partial c}{\partial r} \tag{6}$$

$$r = 1, \ c = c_{lim} \tag{7}$$

$$r = \rho, \ -\frac{\partial c}{\partial r} + \frac{2v}{\rho}c = 0 \tag{8}$$

Table 1. Correspondence between absolute and dimensionless symbols.

Symbols	Name	Dimension	Dimension-less symbol
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} day^{-1}	$\omega = -\rho^2\theta\beta/(2\phi\eta)$
C	nutrient concentration	mg ml^{-1}	$c = C/C_i$
C_{lim}	limiting concentration	mg ml^{-1}	$c_{lim} = C_{lim}/C_i$
ϕ	supply/demand parameter		ϕ
$\theta\beta$	buffer capacity		$\beta = (K_a+\theta)/\theta$
V	flux of water	cm day^{-1}	$2v = RV/D$

The initial condition transforms into

$$t = 0, \quad c = 1 \tag{9}$$

The exact solution for the concentration at location r and time t is given by (de Willigen & van Noordwijk, in preparation):

$$c = -\pi c_{lim} \sum_{n=0}^{\infty} \frac{2\nu J_\nu^2(\alpha_n) - \alpha_n \rho^{\nu+1} J_\nu(\alpha_n) J_{\nu+1}(\alpha_n)}{J_\nu^2(\alpha_n) - J_{\nu+1}^2(\rho\alpha_n)} \frac{r^\nu C_\nu(r\alpha_n)}{\rho^{\nu+1}\alpha_n} e^{\frac{-\alpha_n^2 t}{\theta\beta}}$$

where:
α_n = the n-th zero of

$$Y_\nu(\alpha) J_{\nu+1}(\rho\alpha) - Y_{\nu+1}(\rho\alpha) J_\nu(\alpha) = 0$$

where $J_\nu(\alpha)$ and $Y_\nu(\alpha)$ denote Bessel functions of the first and second kind respectively, with order ν and argument α.
The uptake rate can be derived as

$$\omega_t = \left(\frac{\partial c}{\partial r}\right)_{r=1} = -2c_{lim} \sum_{n=0}^{\infty} \frac{2\nu J_\nu(\alpha_n) J_{\nu+1}(\rho\alpha_n) - \alpha_n \rho^{\nu+1} J_{\nu+1}^2(\rho\alpha_n)}{\alpha_n \left(J_\nu^2(\alpha_n) - J_{\nu+1}^2(\rho\alpha_n)\right)} e^{\frac{-\alpha_n^2 t}{\theta\beta}} \tag{12}$$

Now it can be shown (de Willigen & van Noordwijk, 1987) that the complicated expression for uptake (Equation 12) can be approximated by a much simpler equation, relating uptake to the average concentration in the soil cylinder,

$$\omega_t = -\frac{(\rho^2-1)}{2G(\rho,\nu)}(\bar{c} - c_{lim}) \tag{13}$$

with

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

$$\frac{(1-\rho^{2\nu+4})(\nu+1)}{(2\nu+4)(\rho^{2\nu+2}-1)}$$

$\bar{c}$ = the average dimensionless concentration in the soil cylinder

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2.2 Nutrient uptake by a root system

2.2.1 One class of representative roots

For a root system consisting of regularly 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 12 and approximated by Equation 13. In absolute units,

$$A_p = L_{rv} 2\pi HR_0 D \left[\frac{\partial C}{\partial R}\right]_{R=R_0} = L_{rv} 2\pi HDC_i \left[\frac{\partial c}{\partial r}\right]_r \tag{15}$$

where:
A_p = potential uptake rate per unit surface (mg cm^{-2} day^{-1})
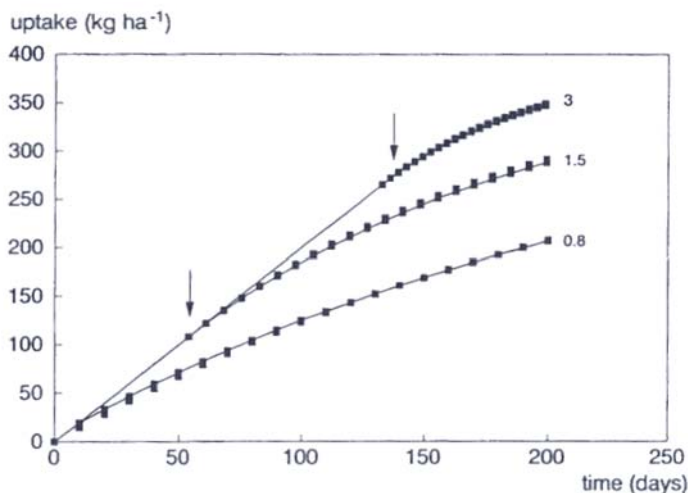L_{rv} = root length density (cm cm^{-3})

Figure 1. *Cumulative uptake calculated with the exact solution (Equation 12) and the steady-rate approximation. Parameters: available amount 400 kg ha^{-1}, required uptake rate 2 kg ha^{-1} day^{-1}, root length 20 cm, root radius 0.02 cm, transpiration 0.5 cm day^{-1}, water content 0.3, diffusion coefficient 0.028 cm^2 day^{-1}, adsorption constant 20, limiting concentration $C_{lim} = 0$. 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 numbers on the curves denote the root length density in cm cm^{-3}. For root density 0.8 cm cm^{-3} zero-sink uptake occurs from time = 0.*

Using the steady-rate approximation A_p, can be given as:

$$A_p = 2\pi \, HDL_{rv}(\bar{C} - C_{lim})\frac{(\rho^2-1)}{2G(\rho,\nu)}$$

If the required uptake rate is given by A_r (mg cm^{-2} day^{-1}), it is assumed that the actual uptake rate A_a equals the required uptake rate as long as this is less than the potential uptake rate, otherwise it equals the potential uptake rate

$$A_a = \begin{matrix} A_r \text{ for } A_r \leq A_p \\ A_p \text{ for } A_r > A_p \end{matrix} \qquad (17)$$

Figure 1 shows the cumulative uptake calculated from the exact solution (Equation 12) and from the steady-rate approximation (Equation 13) for different conditions. It illustrates the closeness of the steady-rate approximation to the exact solution.

The above derivations pertain to a nutrient 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. phosphate (Figure 2) the governing transport equation is non-linear and no analytical solution could be found. To obtain a complete solution one has to resort to numerical methods. Nevertheless it appears that the uptake can be approximated by Equation 13 as well. This is illustrated by Figure 3.
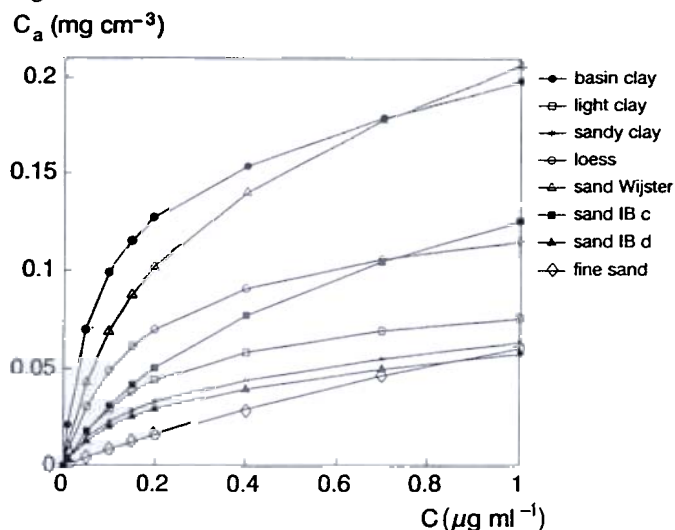
C_a (mg cm^{-3})

Figure 2. Phosphate adsorption isotherms for eight Dutch soils. C_a is adsorbed phosphorus, C is concentration in the soil solution.
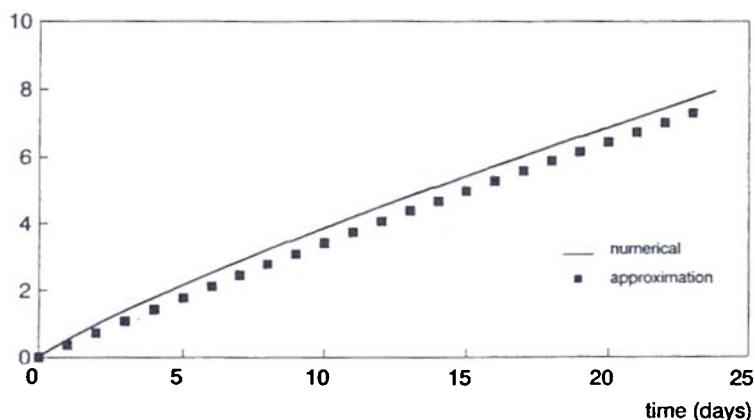
cumulative P uptake (kg ha^{-1})

Figure 3. Cumulative phosphate uptake calculated with the numerical model (line) and with the approximation (points). 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 x 10^{-5} mg ml^{-1}. Transpiration 0.5 cm day^{-1}.

When it can be assumed that relevant parameters, e.g. root length density, required uptake rate, water content, and transpiration, are constant over a certain period, say ΔT_s, Equation 16 offers the possibility to estimate the total supply of nutrient required to ensure adequate uptake of a particular nutrient. At the end of the period the average concentration should at least be such that A_p equals A_r, or

$$\bar{C} = C_{lim} + \frac{2A_r G(\rho, v)}{2\pi HDL_{rv}(\rho^2 - 1)}$$ (18)

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

2.2.2 Non-regularly distributed roots

When different horizontal layers 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 a favourable position can compensate for roots in a less favourable position 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 in an iterative way. 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, uptake from this layer equals the required uptake. If the potential uptake rate is less than the required uptake rate, uptake from this layer equals the potential uptake rate. For convenience those layers where actual uptake equals potential uptake will be indicated as layers of category 1 (i.e. layers in which the roots cannot meet the required uptake per unit root length).

The total uptake by the root system is the sum of the uptake rates of 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 raised to increase total uptake, possibly enough to meet the 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 of those layers (category 2) that were able to satisfy the required uptake rate of step 1. This yields an additional uptake rate. The required uptake rate for layers of category 2, in step 2, now equals the required uptake rate of step 1, augmented with the additional uptake rate. Next it is examined if the layer can satisfy the required uptake, i.e. if its potential uptake rate still exceeds the new value of the required uptake rate. If not, the uptake rate from this layer equals the potential uptake rate. If all layers of category 2 can satisfy the required uptake of step 2, total uptake equals demand and the iteration ends. If none of the layers of category 2 can satisfy the required uptake of step 2, i.e. if in all layers of category 1 and 2 zero-sink uptake occurs, the iteration also ends. If only a part of the layers of category 2 can satisfy the required uptake of 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, as far as uptake is concerned, is instantaneously available throughout the complete root system.

The procedure described above can also be applied when roots within a horizontal layer are not distributed regularly. The layer then is divided over a number of compartments within which root distribution can be assumed to be regular.

3 Modelling uptake of water

3.1 Uptake by a single root

For the single-root model we start by considering a vertical cylindrical root. The root is situated within a cylinder of soil. Over the outer boundary of this cylinder no transport will take 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 the finding of analytical solutions generally very difficult. We had to resort to numerical techniques (fully implicit finite difference scheme, Patankar, 1980) to obtain a solution.

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

$$\Phi = \int_{\theta}^{\theta_{sat}} D_w d\theta = \int_{P}^{0} K dP \qquad (19)$$

where:
K = hydraulic conductivity (cm day^{-1})
P = pressure head (cm)
D = diffusivity (cm^2 day^{-1})
θ = water content (cm^3 cm^{-3})

The steady-rate solution in terms of the matric flux potential reads

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

where:
Φ_{rs} = matric flux potential at the root surface
U_2 = flow of water towards the root

From Equation 20 an expression can be derived giving U_2 as a function of the average matric flux potential in the soil,

$$U_2 = 2\pi H L_{rv}(\Phi_{rs} - \Phi) \frac{\rho^2-1}{2G(\rho,0)} \qquad (21)$$

Note the similarity of Equations 21 and 16. The function $G(\rho,0)$ can be derived from Equation 14 by taking the limit as $v \rightarrow 0$, the result is

$$G(\rho,0) = \frac{1}{2} \left[\frac{-3\rho^2}{4} + \frac{\rho^4 \ln\rho}{\rho^2-1} \right] \qquad (22)$$

Figure 4 shows the time course of water transport to the root in case of constant uptake (0.5 cm day^{-1}) until the pressure head at the root surface P_{rs} drops to 0.5 MPa, thereafter P_{rs} is constant at 0.5 MPa, calculated with the numerical model and with the steady-rate approximation Equation 21. The approximation is shown to be quite satisfactory.

3.2 Uptake by·a root system

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

$$F_w = k_1 (P_{rs} - P_p) + k_2 \tag{23}$$

where:
F_w = flux of water into a cm root in (cm^3 day^{-1})
P_{rs} = pressure head in the soil at the root surface (cm)
P_p = plant water potential (cm)
k_1 = coefficient related to the root conductivity (cm day^{-1})
k_2 = coefficient related to the root conductivity (cm^3 day^{-1} per cm root)

$$\frac{cm^3 (water)}{cm (root) \cdot cm (water\ pot) \cdot day}$$

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

$$U_1 = L_{rv} \Delta x F_w = q(P_{rs} - P_p) + v \tag{24}$$

where: assume v = 0

$$q = L_{rv} \Delta x k_1, \text{ and } v = L_{rv} \Delta x k_2 \tag{25}$$
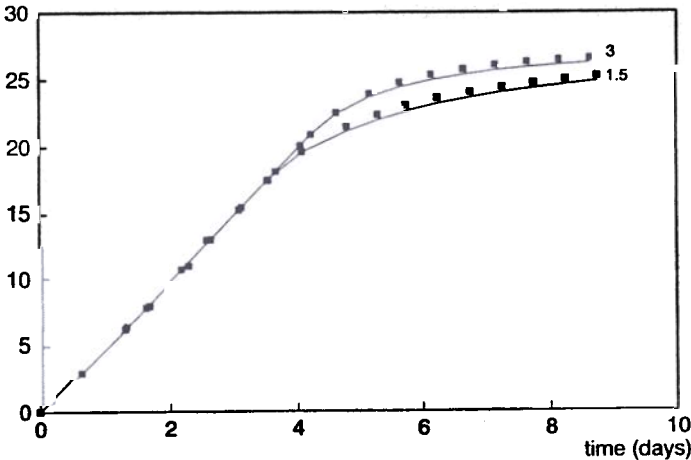
water transport cum. (cm)

Figure 4. Cumulative transpiration water transport calculated with the numerical model (lines) and with the approximation (points). Transpiration was set constant at 0.5 cm day^{-1}, until the pressure head at root surface the reaches 5000 cm. Thereafter the pressure head is kept constant at 5000 cm. The numbers on curves denote the root length density cm (cm^{-3}).

We assume that no water can accumulate at the root surface, so that U_1 equals the supply of water at the root surface. 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

$$U_2 = s(\Phi_{rs} - \Phi) \tag{2}$$

where:

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

whereas a functional relationship exists between Φ and P (see definition of Φ in Equation 19).

If the required uptake is given as E_{act} (transpiration rate in (cm day^{-1})) the right hand side of Equation 26 should equal E_{act}, and the resulting equation can simply be solved for Φ_{rs}. Using the inverse of Equation 19 then P_{rs} is calculated. Finally, because

$$U_1 = U_2 = E_{act} \tag{28}$$

the plant water potential can be computed from Equation 24 as

$$P_p = P_{rs} - (E_{act} - v)/q \tag{29}$$

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

$$E_{act} = f(P_p) E_{pot} \tag{30}$$

where:
$f(P_p)$ = 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 can be assumed to be distributed regularly within a layer, for each layer equations like Equations 24 and 26 can be formulated. Equating these equations one finds for the ith layer

$$q_i(P_{rs,i} - P_p) + v_i = s_i (\Phi_{rs,i} - \Phi_i) \tag{31}$$

It is assumed that the plant water potential P_p is identical everywhere in the root system. In total there are n equations of the form of Equation 31, and n+1 unknowns i.e. $P_{rs,1}$ - $P_{rs,n}$ (where again Equation 19 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 in each layer from the root zone equals E_{act}:

$$\sum_{i=1}^{n} q_i(P_{rs,i} - P_p) + v_i = E_{act} \tag{32}$$

When one takes into account the relation between plant water potential and uptake rate Equation 30 has to be used. Because of the nonlinearity of Equations 19 and 30 again the solution has to be found by iteration.

4 Results and discussion

4.1 Required phosphate level in the soil for different crops

The phosphate recommendation for arable crops in the Netherlands is based on the so-called Pw-value of the plough layer (the upper 20-25 cm of the soil profile). This value gives the amount of phosphate, 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 18 to calculate the minimum required phosphate 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
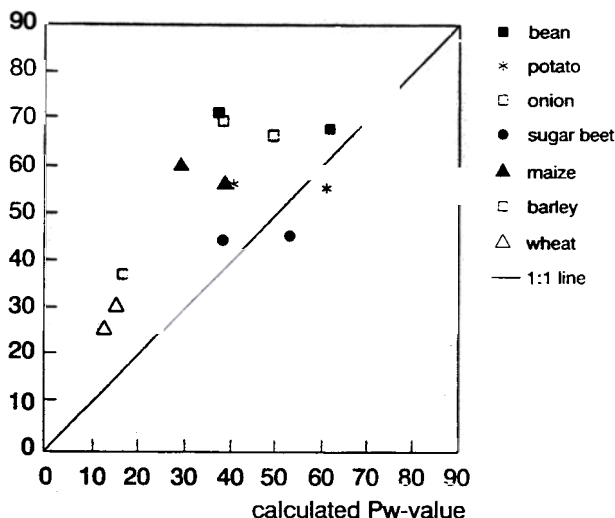

Figure 5. *Comparison of the required Pw-value calculated with Equation 18 and required Pw-value as estimated from results of field experiments.*

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required phosphate supply. For each crop representative values for daily P demand and root length density were used. Figure 5 presents the results. Although the agreement between theoretical and experimental results is not 1:1, the correlation between the two is considerable. This at least indicates that the P level in the soil necessary to meet the phosphate requirement of crops can be estimated with Equation 18.

4.2 Nitrogen uptake by a maize crop in the humid tropics

De Willigen & van Noordwijk (1989) applied the procedure explained in Section 2.2.2 to describe nitrogen uptake of a maize crop growing under humid tropical conditions. Calculations were based on measured root length densities in various layers. Heterogeneous root distribution in a horizontal plane was taken into account. Daily crop nitrogen demand was calculated with a submodel on crop growth and required crop nitrogen content. Figure 6 shows some results.

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

The model described in Section 3.2 was tested with data of Sharp & Davies (1985) who performed an experiment with maize plants. They grew eighty plants 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
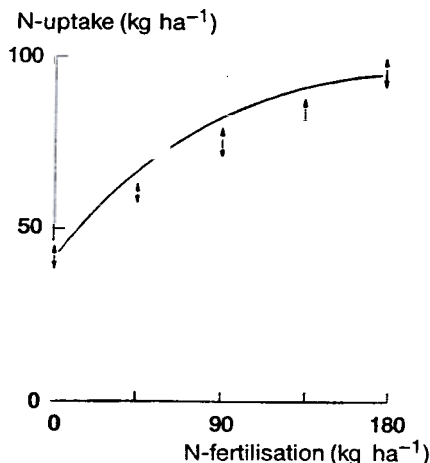

Figure 6. Nitrogen uptake as a function of N fertilization in experiments at Onne (S.E. Nigeria). Calculated uptake (line) is compared with experimental results; the arrows indicate the range of the experimental results.

all. Every three days some columns were harvested and soil water content, root
length distribution, total dry matter and its distribution were measured, as well as,
prior to harvesting, the leaf water potential. Soil water depletion rates were
calculated from the changes in soil water content between successive sampling days.

No data on diffusivity as a function of water content were given, and the
information about the moisture retention curve is rather incomplete. Nevertheless, the
data can be used to illustrate the performance of the model. To this end the model
was run with data on hydraulic properties of a peat soil (B18, Wösten, 1989). 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 the 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 highest root density but in the lower layers where the
moisture content is considerably higher than in the upper layers. The model predicts
similar distributions of water uptake as were observed experimentally .

4.4 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 explored. As an example a soil
profile of 90 cm is considered as consisting of three layers of 30 cm each. The root
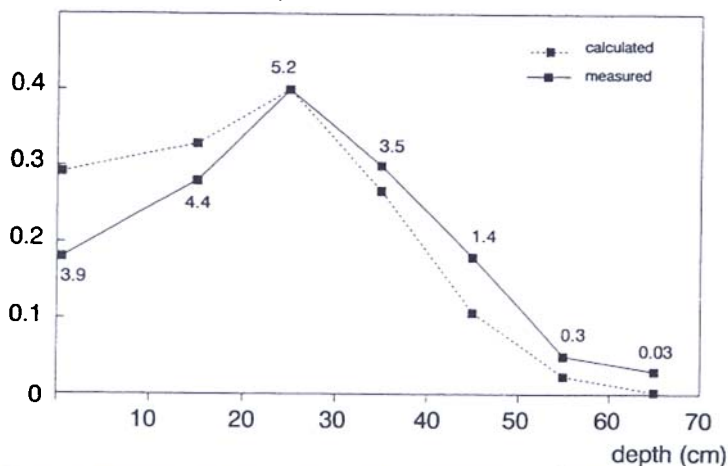density in these layers amounted to 1.5, 0.7 and 0.2 cm cm^{-3} respectively,

Figure 7. Measured and calculated depth-distribution of water uptake lines and root length density
of maize plants in a soil kept at field capacity. Data from Sharp & Davies (1985). For the
calculations a root conductivity (k_l) of 10^{-5} cm day^{-1} was used. The numbers at the points
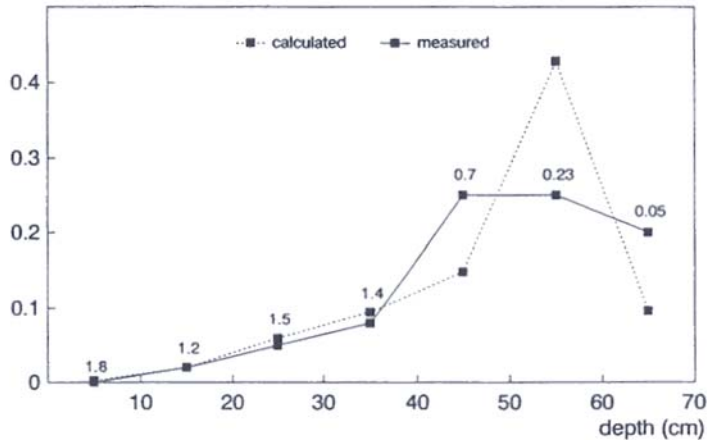denote the root length density (cm cm^{-3}).

water uptake

Figure 8. As Figure 7, but in a soil which has not been watered during 15 days.

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). As Table 2 shows the water uptake in the upper layer hardly contributes to total transpirational demand, but this can be met by the uptake of the roots in the lower layers. One can expect that the nitrate is concentrated in the upper layer, because it is applied at the surface and its downwards movement during the growing season will be limited because evapotranspiration exceeds precipitation. In such conditions the uptake of nitrogen in the upper layer is seriously restricted, 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 day^{-1})
	1.5	2000	0.0032
	0.7	-200	0.379
	0.2	-100	0.118

Plant water potential	: 2000 cm
Transpiration	: 0.5 cm day

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 day^{-1})	N uptake (kg ha^{-1} day^{-1})	N content (kg ha^{-1})
0-30	1.5	1.32 x 10^{-3}	2.08	50
30-60	0.7	9.98 x 10^{-2}	0.50	
60-90	0.2	0.151	0.15	

Nitrogen demand: 6 kg ha^{-1} day^{-1}
Nitrogen uptake: 2.7 kg ha^{-1} day$^-$

When the upper layer has the same pressure head as the second layer (200 cm) most water is extracted from 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 have been the case even if transport was by diffusion only (Table 6).

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 day^{-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 day^{-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 day^{-1})	N uptake (kg ha^{-1} day^{-1})	N content (kg ha^{-1})
0-30	1.5	9.98 x 10^{-2}	5.37	50
30-60	0.7	9.98 x 10^{-2}	0.49	1
60-90	0.2	0.151	0.15	1

Nitrogen demand: 6 kg ha^{-1} day^{-1}
Nitrogen uptake : 6 kg ha^{-1} day^{-1}

Table 6. Distribution of nitrogen uptake with depth and total nitrogen uptake for the soil water situation of Table 4, but in absence of transpiration. Nitrate mainly concentrated in upper layer.

Depth (cm)	Root density (cm cm^{-3})	Diffusion coefficient (cm^2 day^{-1})	N uptake (kg ha^{-1} day^{-1})	N content (kg ha^{-1})
0-30	1.5	9.98 x 10^{-2}	5.37	50
30-60	0.7	9.98 x 10^{-2}	0.49	1
60-90	0.2	0.151	0.15	1

Nitrogen demand: 6 kg ha^{-1} day^{-1}
Nitrogen uptake : 6 kg ha^{-1} day^{-1}

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. Again, the nitrogen demand can be met in full.

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 (cm)	Root density (cm cm^{-3})	Diffusion coefficient (cm^2 day^{-1})	N uptake (kg ha^{-1} day^{-1})	N content (kg ha^{-1})
0-30	1.5	1.32 x 10^{-3}	0.042	1
30-60	0.7	9.98 x 10^{-2}	5.81	50
60-90	0.2	0.151	0.15	1

Nitrogen demand: 6 kg ha^{-1} day^{-1}
Nitrogen uptake : 6 kg ha^{-1} day^{-1}

The last example qualitatively agrees with experimental results of Garwood & Williams (1967), who applied nitrogen in a dry period 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 greater for nitrogen injected at this depth than for surface applied nitrogen.

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

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

The examples show that situations can 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 of nutrients in the soil. This implies that estimates of crop production made with models based on water uptake alone, e.g. to evaluate the effect of improved drainage resulting in

lowering of the ground water table, should be treated with caution. Such models could predict unrestricted growth due to adequate water supply when the lower layers of the root zone are reasonably moist but would overlook the possibility of nutrient deficiency in drier upper layers.

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