Simulation of nutrient uptake by a growing root system considering increasing root density and inter-root competition

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Abstract

A simulation model is presented which describes uptake of a growth limiting nutrient from soil by a growing root system. The root surface is supposed to behave like a zero-sink. Uptake of the nutrient is therefore determined by the rate of nutrient supply to the root surface by mass flow and diffusion. Inter-root competition and time dependent root density are accounted for by assigning to each root a finite cylindrical soil volume that delivers nutrients. The radius of these cylinders declines with increasing root density. Experiments with rape plants grown on quartz sand were used to evaluate the model. Simulated nitrogen uptake agreed well with observed uptake under nitrogen limiting conditions. In case no nitrogen limitation occurred nitrogen uptake was overestimated by the model, probably because the roots did not behave like a zero-sink any more.

Introduction

Simulation models for nutrient uptake have frequently been used in the evaluation of the effect of soil and root characteristics on nutrient uptake. Uptake models allowing for growing roots were developed by Nye *et al.* (1975), Claassen and Barber (1976) and Cushman (1979). No effects of time dependent root density on inter-root competition are included in these models. This hampers their use in the simulation of experiments with rapidly increasing root densities, as usually found in pot experiments.

Claassen and Barber did not include inter-root competition because they assumed that roots exploit a cylindrical soil volume with a constant solute concentration at the outer boundary. Their model overestimates nutrient uptake if nutrients are mobile (Silberbush and Barber, 1983). In Cushman's model the cylinder wall is impermeable to nutrients and the nutrient concentration at the cylinder wall declines in consequence of uptake. Though root growth is considered in this model, root density is kept constant in time *i.e.* the soil volume available per unit root length does not change with increasing root length. Therefore, in a situation with high root growth rates, this model also overestimates nutrient uptake (Silberbush and Barber, 1983). Baldwin *et al.* (1973) proposed an equation to extend Nye's model in which the effect of increasing root density on inter-root competition is described: the radius of each finite soil volume surrounding a root is a function of root density, assuming that each newly formed root samples the mean nutrient concentration. The validity of this assumption is questionable, because it is well established that roots branch mostly in zones of highest nutrient concentration (Russell, 1977). Yet, Nye's model was only tested under condi-

tions where inter-root competition was not expected so that the equation of Baldwin *et al.* was not included in the model. Overestimation of nutrient uptake by Nye's model was again attributed to inter-root competition (Brewster *et al.*, 1975).

The objective of this paper is to present a new simulation methodology that considers inter-root competition in a soil with increasing root density. Simulation results and experimental data will be compared.

Methods

Theoretical

The simulation model developed describes nutrient uptake by a root system that grows in a restricted soil volume. Each root is assigned a finite cylindrical soil volume delivering nutrients, and the soil volume per unit root length declines with increasing root density. Uptake of nutrients by the root, transport of nutrients to the root surface and the effect of increasing root density are considered as the three main components of this model and will be described subsequently.

Each timestep, the equation of continuity for cylindrical co-ordinates is solved:

$$\frac{\delta C}{\delta t} = -\frac{1}{r} \times \frac{\delta}{\delta r}(r \times F) + S \quad \text{(Eq. 1.9 in Nye and Tinker, 1977)}$$

The initial boundary condition is described by:

$$t = 0 \quad r > r_0 \quad C = C_i$$

The sink term S represents nutrient uptake by the root that is situated in the centre of a soil cylinder. All nutrients arriving at the root surface are supposed to be absorbed, *i.e.* the root surface is supposed to behave like a zero-sink. Root hairs are assumed to be so abundantly present that they are regarded to enlarge the root surfacial area to one located near their tips (Nye, 1966). The boundary condition at the tips of the root hairs is therefore:

$$t > 0 \quad r = r_0 \quad C_0 = 0$$

The rate of nutrient supply to the root surface by mass flow and diffusion is described according

List of symbols		
symbol	definition	units
A	total surface area of the pot	cm^2
C	ion concentration in soil solution	$\mu mol \times cm^{-3}$
C_0	ion concentration in the soil solution at the root surface	$\mu mol \times cm^{-3}$
C_i	initial ion concentration in the soil solution	$\mu mol \times cm^{-3}$
D_0	diffusion coefficient of ion in free solution	$cm^2 \times day^{-1}$
D_e	effective diffusion coefficient	$cm^2 \times day^{-1}$
F	flux of nutrients to root surface	$\mu mol \times cm^{-2} \times day^{-1}$
F_1	total flux of the nutrient across the outer boundary of the soil cylinder	$\mu mol \times cm^{-2} \times day^{-1}$
f	tortuosity factor	–
L_c	critical root length	cm
M_t	amount of P on infinite sink	$\mu mol \times cm^{-2}$
n	number of plants per pot	–
r	radial distance from root axis	cm
r_0	root radius + root hair length	cm
r_1	radius of the soil cylinder surrounding each root	cm
S	sink term	$\mu mol \times cm^{-3} \times day^{-1}$
t	time	day
V_1	total volume of the pot or soil layer considered	cm^3
v	inward water flux	$cm^3 \times cm^{-2} \times day^{-1}$
v_0	water flux across the root surface	$cm^3 \times cm^{-2} \times day^{-1}$
v_1	water flux across the outer boundary of the soil cylinder	$cm^3 \times cm^{-2} \times day^{-1}$
θ	volumetric moisture content	$cm^3 \times cm^{-3}$

to

$$F = -D_e \times \frac{dC}{dr} + v \times C \quad \text{(Eq. 1.5 in Nye and}$$
Tinker, 1977)

with

$$D_e = \theta \times f \times D_0 \quad \text{(Nye, 1968)}$$

Buffering of the solute by the soil is not included.

Inter-root competition for nutrients is accounted for by assigning finite cylindrical volumes with radius r_1 to each root. Water but no nutrients can pass the cylinder wall, similarly to Cushman's model. The boundary condition at r_1 is therefore:

$$t > 0 \quad r = r_1 \quad F_1 = 0 \quad v_1 = r_0 \times v_0/r_1$$

The initial radius of each soil cylinder is calculated by

$$t = 0 \quad r_1 = \sqrt{(A/(\pi \times n))}$$

assuming that each plant starts with one root growing in vertical direction. Each of these parallel soil cylinders is divided into a number of concentric compartments (shells). The time course of the concentration of nutrients in the soil solution in each of these shells is described according to the above mentioned equations.

Each time the actual root length exceeds a certain critical root length L_c, the outer shell of each soil cylinder is stripped off and their material is used to form new soil cylinders that are assigned to the newly developing roots. These new cylinders have the same radius as the older ones after stripping and they are divided into the same number of shells as left over in the stripped cylinders.

The solute concentration in the newly formed soil cylinders is initially the same as that in the outer stripped shells, where the nutrient concentrations are highest. This can be interpreted as new roots penetrating between older ones, in zones of highest nutrient concentration. After formation, a new time dependent nutrient concentration gradient is calculated in each soil cylinder.

The critical root length L_c is a function of the current radius of the soil cylinder surrounding each root, according to the following equation:

$$L_c = V_1/(\pi \times r_1^2)$$

Up to the first moment that a critical root length is reached and the stripping procedure is executed, the uptake calculation takes place with a root length that is half of the first critical root length. After reaching the first critical root length, the calculations are performed with the arithmetic average of the previous and newly calculated critical root length. Therefore, during the first half of each period nutrient uptake is overestimated, whereas during the last one it is underestimated. On the average this should yield reasonable results. This method spares CPU-time in comparison with a method by which uptake is calculated with the actual root length.

Additional conditions for which the model was developed are: neither temporal nor spatial gradients in volumetric moisture content occur, there is no nutrient production, no spatial gradient in root density and nutrient uptake is homogeneous along the root.

Plant parameters needed to run the model are: root length as a function of time, radius of the root, root hair length and the water uptake per unit root length as a function of time. Soil parameters needed are: the volumetric water content θ, the tortuosity factor f, D_0 and the initial concentration C_i of the nutrient.

The CSMP-III simulation model was executed on a VAX computer using the variable time step integration method of Runge-Kutta Simpson. A copy of the model is available at request from the first authoress (E.H.).

Experimental

Experiments were done to provide the above mentioned soil and plant parameters for the model and to evaluate the model by comparing predicted nitrate uptake with observed nitrate uptake by rape plants growing in cylindrical pots on quartz sand.

Measurement of f as function of θ   The relation between the tortuosity factor f and θ was de-

termined by a method similar to that described by Vaidyanathan and Nye (1966). Iron oxide paper (2×4 cm; see Van der Zee et al., 1987) was used as an "infinite sink" for phosphate ions. Quartz sand was washed with $1.5\,M$ HCl and demineralized water respectively and subsequently heated at 900°C to make it inert with respect to phosphate so that the behaviour of phosphate did not differ essentially from that of nitrate. The pretreated sand was mixed with a nutrient solution containing $5.0\,\text{m}M$ KH_2PO_4 and packed into Petri dishes (dry bulk density $1.28\,\text{g} \times \text{cm}^{-3}$) with a piece of iron oxide paper on the bottom. The moisture content of the iron oxide paper had previously been equilibrated with quartz sand that was moistened with demineralized water up to the desired θ. To prevent sagging of the nutrient solution, the dishes were placed in an end-over-end shaker. After about 3 hours contact time the iron oxide paper was removed, washed in demineralized water, air dried, and extracted in 5 ml $0.2\,M$ H_2SO_4. The extract was analyzed for phosphate by the molybdenum-blue method. D_e was then calculated from the amount of phosphate on the paper by

$$D_e = \frac{\pi \times M_t^2}{4 \times C^2 \times t} \quad \text{(derived from Eq. 3.15 in Crank, 1975)}$$

and f by

$$f = \frac{D_e}{\theta \times D_0} \quad \text{(derived from Nye, 1968)}.$$

Plant growth Rape plants (*Brassica napus* L. cv. Jetneuf) were grown for 16 days on quartz sand in cylindrical pots at two nitrate levels. Ten plants of rape were grown in 3-1 pots (ϕ 12 cm, height 27 cm). Each pot contained a mixture of 3.2 kg quartz sand (dry bulk density $1.28\,\text{g} \times \text{cm}^{-3}$) and 575 ml (high moisture level) or 385 ml (low moisture level) nutrient solution. In the $1.5\,\text{m}M$-treatment $1.5\,\text{m}M$ KNO_3 and $3.5\,\text{m}M$ KCl were added to the nutrient solution which consisted of $5.0\,\text{m}M$ $CaCl_2$, $2.0\,\text{m}M$ $MgSO_4$, $2.0\,\text{m}M$ KH_2PO_4 and trace elements (in mg L^{-1}): Fe (as FeEDTA) 4.6; B 0.5; Mn 0.5; Zn 0.05; Cu 0.02; Mo 0.01. In the $5.0\,\text{m}M$-treatment

$5.0\,\text{m}M$ KNO_3 was added. The plants were grown in a growth chamber at 20°C, a 16 h light ($70\,\text{W} \times \text{m}^{-2}$)-8 h dark cycle and a relative humidity of about 80%. Evaporation (from blanc pots) and evapotranspiration were measured daily and the moisture level was readjusted daily. The beginning of the experiment, t = 0 was defined as the moment at which half of the plants was germinated. At each harvest, a number of pots was deep frozen and divided into five layers of 4.5 cm height by sawing. The layers are referred to as layer I through V, from top to bottom. Root length, θ and nitrate concentration in the soil solution were measured in each layer. Nitrate was measured after extraction of dried sand by automatic spectrophotometry after reduction to nitrite. From other pots, plant material was dried and analyzed for N after wet digestion in a H_2SO_4-Se-salicylic acid mixture with addition of H_2O_2. Total N was determined by the indophenol blue method.

Results

Experimental

Measurement of f as function of θ The value of f for different volumetric moisture contents is shown in Figure 1.

Plant growth Substantial differences in volumetric moisture content θ (Table 1) and in the nitrate concentration in the soil solution (Table 2) were found among the five layers of one pot. In pots without plants neither of these two gradients changed significantly during the experiment. Differences of θ with depth resulted from the poor water holding capacity of the quartz sand used. The difference in N concentration among layers is probably caused by the fact that evaporation from layer I was compensated by supplying demineralized water via a tube positioned with its bottom in layer II.

Also considerable difference in root length among the layers (Table 3) was found within one treatment. There was no difference among the five layers with respect to root radius (0.02 cm) and root hair length (± 0.05 cm).
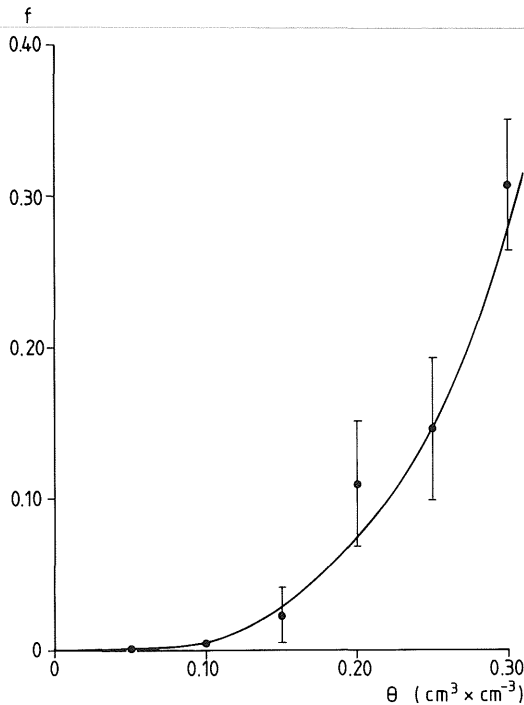
Water uptake per cm root declined from

Fig. 1. Experimentally determined relation between f and θ (means $\pm$s.d., $n = 5$) and relation used in the simulation model (———).

Table 1. Volumetric water content per layer for each treatment. Values are means of two replicates

N level (mM):	1.5	5.0	5.0
Moisture level:	high	high	low
Layer	Volumetric water content (cm$^3 \times$ cm^{-3})		
I	0.13	0.13	0.10
II	0.19	0.19	0.08
III	0.23	0.23	0.15
IV	0.28	0.28	0.17
V	0.30	0.30	0.21

Table 2. Concentration N in the soil solution per layer at $t = 0$ for each treatment. Values are means of two replicates

N level (mM):	1.5	5.0	5.0
Moisture level:	high	high	low
Layer	N concentration in soil solution (mM)		
I	2.6	9.6	7.7
II	0.5	2.7	1.9
III	1.2	3.9	4.9
IV	1.3	5.6	6.4
V	1.6	5.1	4.8

$0.028 \, \text{cm}^3 \times \text{day}^{-1}$ at the beginning of the experiment to $0.002 \, \text{cm}^3 \times \text{day}^{-1}$ at the end. No significant differences were found among the three treatments.

Total N uptake per pot and tissue N concentration as a function of time for each treatment are depicted in Figures 2 and 3, respectively. In the high moisture level treatments no nitrate was left in the soil solution at the end of the experiment, while in the low moisture level treatment about 30% of the added nitrogen was left in the nutrient solution (mainly in layers IV and V).

Simulation

To approximate the model conditions of absence of spatial gradients in moisture level and root density, the simulation model was run for each of the five soil layers considered in the experiment. Total N uptake per pot was calculated by summation.

Soil parameters presented in Table 1 and Figure 1 were used to run the model. The simulation was initialized with respect to the N concentration in the soil solution with data given in

Table 3. Root length per layer as a function of time for each treatment. Values are means of two replicates.

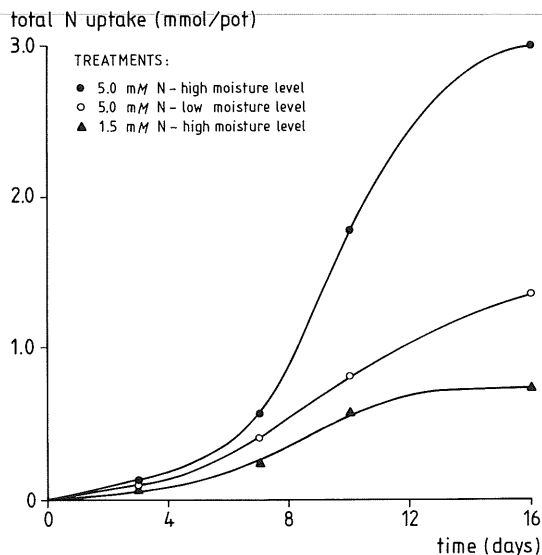| Layer	1.5 mM N high moisture level					5.0 mM N high moisture level					5.0 mM N low moisture level				
	Root length (m) after 0, 3, 7, 10 or 16 days														
	0	3	7	10	16	0	3	7	10	16	0	3	7	10	16
I	0.3	1.6	5.0	6.4	12.5	0.3	1.2	6.4	8.4	24.8	0.3	0.3	4.3	7.2	10.0
II	0.1	0.5	3.7	4.1	6.6	0.1	0.3	3.5	7.2	10.9	0.1	0.1	2.5	7.1	5.5
III	0.0	0.2	2.8	4.5	8.3	0.0	0.2	3.3	7.2	17.0	0.0	0.0	1.9	9.3	11.8
IV	0.0	0.1	1.4	4.2	11.7	0.0	0.1	2.3	5.7	19.1	0.0	0.0	1.4	8.0	17.7
V	0.0	0.0	0.8	2.0	19.7	0.0	0.1	0.8	4.0	41.7	0.0	0.0	0.6	3.9	25.1

Fig. 2. N uptake by rape plants grown on quartz sand as a function of time. Values are means of three replicates.

Table 2. Root length (Table 3) and water uptake per cm root as a function of time were used as forcing functions. The initial number of shells surrounding a root was set to 27. During the simulation period this number declined to 1 at t = 16 days in consequence of root growth.
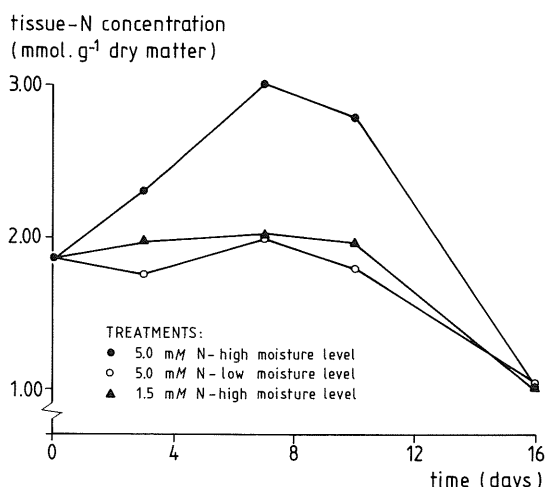
Predicted and observed N uptake are shown in Figure 4.

Fig. 3. N concentration in dry matter of rape plants grown on quartz sand as a function of time. Values are means of three replicates.
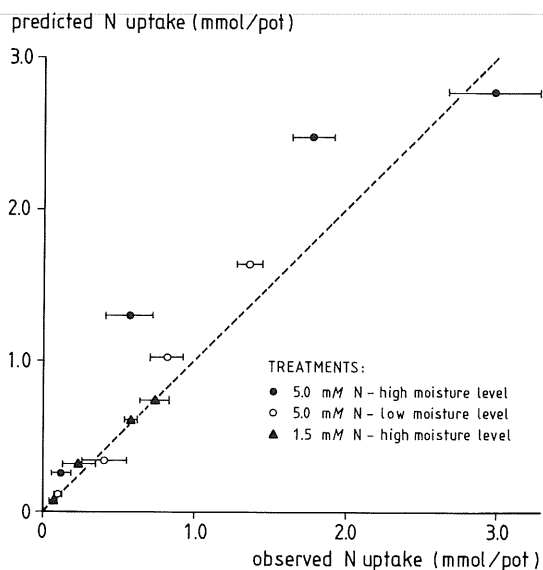

Fig. 4. Comparison of observed N uptake (means ±s.d., $n = 3$) by rape with predicted N uptake for three treatments. The dashed line is where predicted uptake equals observed uptake.

Discussion

Comparison of predicted N uptake with observed uptake (Fig. 4) shows good agreement for the 1.5 mM-high moisture level and 5.0 mM-low moisture level treatment. When predicted and observed N uptake are compared per layer (data not shown) for the 1.5 mM-high moisture level treatment, there is a close agreement in each layer. This means that both nutrient transport to the root surface and the effect of increasing root density on nutrient uptake are simulated well. In the 5.0 mM-low moisture level treatment a slight overestimation of N uptake occurs after 10 days of growth. This overestimation originates from layer IV and V, with relatively high amounts of N available in the soil solution.

The model overestimates N uptake for the 5.0 mM-high moisture level treatment (Fig. 4). Figure 3 shows that tissue N concentration in this treatment at t = 7 and t = 10 days is about $3 \, mmol \times g^{-1}$ dry matter, which is the concentration of N sufficient rape plants (Hoffland *et al.*, 1989). Nitrate was apparently not growth limiting and therefore, it is very likely that the model assumption that roots act like a zero-sink is not met under these conditions. This will cause

an overestimation of N uptake. The model should be extended with a description of biologically controlled nutrient uptake to simulate uptake under these conditions. No effort has been made to describe nutrient uptake by first order or Michaelis-Menten kinetics, because too little is known about the required parameters and their dependence on root age, state of development of the plant and nutrient status of the plant.

The satisfactory prediction of N uptake in cases where N is growth limiting throughout the experiment indicates that the presented equations that describe the effects of inter-root competition and increasing root density on nutrient uptake are powerful.

Acknowledgements

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