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REGULAR ARTICLE

Comparing different approaches to calculate the effects of heterogeneous root distribution on nutrient uptake: a case study on subsoil nitrate uptake by a barley root system

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Abstract Simulation models of nutrient uptake of root systems starting with one-dimensional single root approaches up to complex three-dimensional models are increasingly used for examining the interacting of root distribution and nutrient uptake. However, their accuracy was seldom systematically tested. The objective of the study is to compare one-dimensional and two-dimensional modelling approaches and to test their applicability for simulation of nutrient uptake of heterogeneously distributed root systems giving particular attention to the impact of spatial resolution. Therefore, a field experiment was carried out with spring barley (*Hordeum vulgare* L. cv. Barke) in order to obtain data of in situ root distribution patterns as model input. Results indicate that a comparable coarse spatial resolution can be used with sufficient modelling results when a steady state approximation is applied to the sink cells of the two-dimensional model. Furthermore, the accuracy of the model was clearly improved compared to a simple zero sink approach assuming both near zero concentrations within the sink cell and a linear gradient between the sink cell and its adjacent neighbours. However, for modelling nitrate uptake of a heterogeneous root system a minimum number of grid cells is still necessary. The tested single root approach provided a computational efficient opportunity to simulate nitrate uptake of an irregular distributed root system. Nevertheless, two-dimensional models are better suited for a number of applications (e.g. surveys made on the impact of soil heterogeneity on plant nutrient uptake). Different settings for the suggested modelling techniques are discussed.

Keywords *Hordeum vulgare* L. · Model · Nutrient uptake · Root distribution · Spatial resolution

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Introduction

It has often been pointed out that the variability of root length density (L_v) plays an important role in nutrient and water uptake by plants (Baldwin et al. 1972; Claassen and Steingrobe 1999; de Willigen and van Noordwijk 1987a; Rappoldt 1992; Tardieu et al. 1992; Wang and Smith 2004). Variability of root length density is a basic feature of root systems and can be caused by both genotype and environmental factors. Genetically determined branching patterns have major impact on heterogeneous root distribution (Fitter et al. 1991). However, chemical and physical properties of the soil, which vary frequently on very short distances, are also important (Drew and Saker 1975; Drew and Saker 1978; Hutchings et al. 2003;

Ishaq et al. 2003; Pregitzer et al. 1993; see Doussan et al. (2003) and Robinson (1994) for review). Roots are often accumulated in certain regions (clustering) and root distribution frequently varies on short spatial scales (Tardieu 1988b).

Simulation modelling can be an important means for understanding the influence of the complex dynamics of heterogeneous root distribution on nutrient uptake by plants. However, the complex geometry makes it often necessary to apply simplifying assumptions. This holds in particular for simulation modelling at the crop scale. Nutrient transport therefore is calculated by one-dimensional, two-dimensional and three-dimensional models differing in their level of simplification, see de Willigen et al. (2000), Silberbush (2002) and Wang and Smith (2004) for review.

One-dimensional models often employ the so-called single-root approach, which originates from the steady state model by Gardner (1960) designed originally to model water transport to a single root, which is surrounded by a cylinder of soil.

This methodology was adapted for simulating solute transport to the root surface (Nye and Spiers 1964). Since these initial steps, many refined single root models were constructed (Baldwin et al. 1973; Barber and Cushman 1981; Claassen and Barber 1976; Cushman 1979; Hoffland et al. 1990; Itoh and Barber 1983; Lehto et al. 2006; Nye and Marriott 1969; Smethurst et al. 1993; Yanai 1994). An important amendment was the implementation of inter-root competition. As an approximation, a root system was described as an arrangement of parallel roots, which may compete among one another. Each root is assumed to be located in the centre of a finite soil cylinder (the so-called single root cylinder). However, single root models per se do not account for heterogeneous root distribution in horizontal direction, i.e. within a soil layer. This implies that all single root cylinders are assumed to be equal, which is obviously a crude simplification of the real situation. Fortunately, there are also methods at hand to adopt the single root approach for calculating uptake of a non-regular distributed root system by regarding the root system as a population of cylinders with different radii (Barley 1970; Comerford et al. 1994; de Willigen and van Noordwijk 1987a). Thereby the radii of the soil cylinders and resulting nitrate uptake can be calculated separately for each root.

Additionally multidimensional numerical transport models considering water or nutrient movement in two or three spatial dimensions were developed mainly during the last decade (Annandale et al. 2003; Benjamin et al. 1996; Bruckler et al. 2004; Craine 2006; Craine et al. 2005; Dunbabin et al. 2002a; Somma et al. 1997, 1998; Timlin and Pachepsky 1997; Vrugt et al. 2001a, b; Wang et al. 2002).

This approach generally supports nutrient and water uptake calculations of root systems arranged in non-regular patterns. Multidimensional transport models usually utilise either a two-dimensional grid or a system of rectangular three-dimensional volume cells (Voxel) in order to calculate solute transport. As a rule, grid spacing is mostly uniform and fixed a priori, i.e. there is no readjustment of grid or volume cells with reference to a growing root system. The definition of an appropriate spatial resolution for the raster of these models is a common problem, which is particularly important when dealing with a clustered root system, where distances between root positions may vary in the order of magnitudes. High spatial resolution may improve the accuracy of the model results because of a better geometric representation of the real system but it often leads to increasing simulation time and may cause numerical instability.

However, applying a steady state approximation for calculating the sink term within grid cells containing at least one root may be a promising approach to cope with the problem of spatial resolution.

The above given models have been developed separately for specific conditions and a systematic comparison of the models is still lacking. Therefore, the aim of this study is to compare and to evaluate different approaches to simulate nitrate transport and uptake for heterogeneous root distributions: on the one hand a two-dimensional and on the other hand the one-dimensional approach. Particular importance was given to the impact of spatial resolution on nitrate uptake calculated by using the two-dimensional modelling approach.

Our comparison is based on exemplary calculations of nitrate uptake of an observed barley root system from the subsoil. The results are further discussed with regard to different applications when modelling specific cropping systems.

Materials and methods

Observed root distribution patterns from a field experiment

Determination of in situ root distribution patterns used as model input was carried out with spring barley (*Hordeum vulgare* L., cv. Barke). A field experiment was established in 2004 at the experimental farm Hohenschulen of the University of Kiel (54°19′ N, 9° 58′ E). Soil at this site is a sandy loam (66% sand, 27% silt, 7% clay). On April 2, barley was sown at 330 seeds m^{-2} using a commercial seeder with 0.1 m row width. Nitrogen fertilisation was given at a rate of 90 kg N ha^{-1} in one dose as calcium ammonium nitrate (CAN) with 27% N on April 15. Insects, fungal diseases and weeds were chemically controlled in case of need. Pits were dug in order to obtain the time course of root distribution of spring barley. The roots were exposed at a vertical plane (1 m^2) and mapped in their natural position by use of the foil method according to Böhm (1979) (van Noordwijk et al. 2000) (Fig. 1a). Each map was digitalized using a scanner (Large format scanner FSS 10000, Contex). In order to facilitate analysis of scanned images, a software has been developed which calculates Cartesian coordinates of root intersections and stores acquired data in ASCII formatted data files.

In order to acquire data to parameterize the one-dimensional model, Dirichlet tessellation was carried out for each root on the map resulting in calculated catchment areas, the so-called Voronoi polygons (Fig 1b). The distance between any point within the polygon and the root defining the polygon is shorter than to any other root. Voronoi polygons can be used to describe areas occupied by competing roots arranged in an irregular pattern (Barley 1970; Comerford et al. 1994; van Rees et al. 1994). It was assumed that from any point within the polygon fluxes exist towards the inner sink, i.e. the root, only. There is no flux across the boundary of a Voronoi polygon. The calculations were performed by use of the ArcView Gis 3.3® software (ESRI). Polygons that cut the edge of the considered area were removed.

It was assumed that irregular root distribution has significant effect on nitrate uptake only in case of low root length densities. Therefore, two different distribution patterns from the subsoil were selected. Used root intersection maps were measured at the 72nd and the 86th day after sowing (DAS). Plant development at the sampling date was determined as EC 43 and EC 65, respectively. The selected layers ranged from 0.35–0.80 m depth (Fig. 1) and had a horizontal dimension of 1 m. Mean area values of the catchment areas, coefficients of variation (CV, standard deviation/mean ratio) of the catchment area sizes and mean root length densities were calculated. CV values thereby served as a measure of heterogeneity.

In order to evaluate model performance with respect to a regular root distribution pattern, additional hexagonal distributions were generated with mean root length densities of 0.1 and 1 km m^{-3}, respectively.

Modelling approaches

The aim of the work is to evaluate different model approaches to simulate nitrate transport and uptake for a heterogeneously distributed root system. Based on the continuity equation describing the nutrient dynamics in the soil (de Willigen et al. 2000) simplified one and two dimensional model approaches were derived.

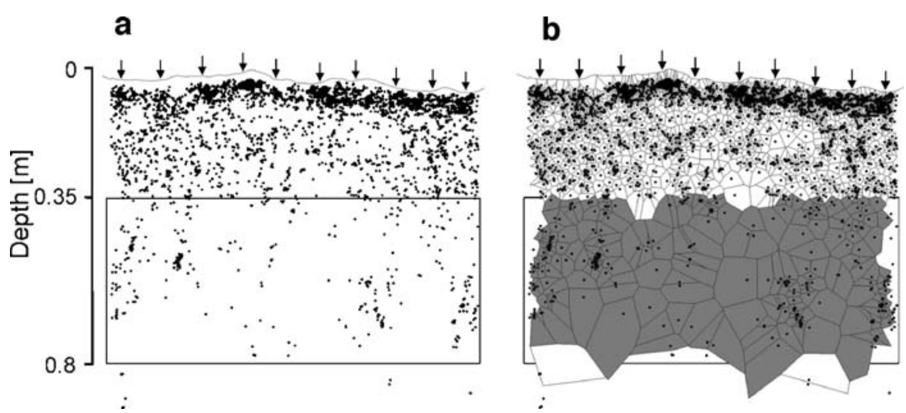

Fig. 1 **a** Root distribution of spring barley obtained by the foil method. **b** Calculated Voronoi polygons (Thiessen map). The layer between 0.35 and 0.80 m is marked by a *rectangle*. Polygons considered for the calculation are highlighted *grey*, polygons which cut the boundaries of the considered area are not drawn. *Arrows* indicate plant rows. Measurement was performed 72 DAS

Inner boundary condition

Nitrate uptake was often calculated by either using Michaelis–Menten kinetics or adopting the approach of de Willigen and van Noordwijk, which assumes that root uptake can be described by a period of constant uptake followed by zero-sink uptake if the demand of the plant cannot be met by nutrient supply of the soil (de Willigen and van Noordwijk 1994a, b).

It has frequently pointed out that plants have the ability to increase nitrate uptake significantly in case of nitrate deficiency (Kirk and Kronzucker 2005; Sharifi and Zebarth 2006; Tinker and Nye 2000).

Under the specific conditions (low total root length in the subsoil in association with a high demand of the plant and transport limited uptake conditions) applied in our study the assumption that the root will behave as a zero sink seems to be justified.

Single root approach adopted for heterogeneous root distribution

If nitrate uptake is limited by the solute transport in the soil, a gradient is built up between the nitrate concentration at the root surface and the nitrate concentration in the bulk soil. Then, diffusion becomes the dominant transport process (Kage 1997) and nitrate transport by mass flow is in most cases not important.

Hence, following Tinker and Nye (2000) the continuity equation can be simplified for calculation of one-dimensional diffusion flow in the single root cylinder:

$$\frac{\partial(\theta C_l)}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(rD_e\theta\frac{\partial C_l}{\partial r} + \pi r^2 P_m\right) \qquad (1)$$

where C_l is the concentration of solute in liquid phase (mol m^{-3}), D_e is the effective diffusion coefficient (m^2 s^{-1}), P_m is the mineralisation rate (mol s^{-1} m^{-3}), t is time (s), θ is the soil moisture fraction by volume (m^3 m^{-3}) and r is the radial coordinate (m).

The term D_e in Eq. 1 is defined as:

$$D_e = D_l\theta f\frac{1}{b} \qquad (2)$$

where D_l denotes the diffusion coefficient of solute in water (m^2 s^{-1}), f is an impedance factor (–) and b is buffering (–). Since $b=\theta$, which holds for ions like nitrate that do not interact with the soil matrix, Eq. 2 simplifies (Tinker and Nye 2000):

$$D_e = D_l f \qquad (3)$$

Even though impedance factor f is dependent on many factors like bulk soil density or soil texture, θ has the most important influence by far (Kaselowsky 1990).

We fit a function on data from Barraclough and Tinker (1981). Because the linear approach gives values of zero for the impedance factor for low water contents, a quadratic function was used. That leads to the following relationship between f and θ:

$$f = 3.35 \times \theta^2 \qquad (4)$$

The inner boundary condition of Eq. 1 is the uptake rate of a single root considering the root surface area. Assuming steady state conditions in a finite cylinder of soil around each root (single root cylinder), the approach developed by Baldwin et al. (1973) offers a solution for Eq. 1. The outside boundary condition at the radius of the cylinder is that of a vanishing flux (Baldwin et al. 1973). This permits simulating uptake of a root system including root competition. In the single root cylinder the average concentration of solute in the liquid phase ($\overline{C_l}$) is calculated according to Baldwin et al. (1973) as:

$$\overline{C_l} = C_{la}\left(1 - \frac{1}{2}\frac{\alpha a}{D_e b} + \frac{r_s^2\frac{\alpha a}{D_e b}}{r_s^2 - a^2}\ln\left(\frac{r_s}{a}\right)\right) \qquad (5)$$

where a denotes the radius of the root axis (m), C_{la} is the concentration of solute at root surface (mol m^{-3}), r_s is the radius of the single root cylinder (m) and α is root absorbing power (m s^{-1}). The term α may be substituted by (Burns 1980):

$$\alpha = \frac{I}{2\pi a C_{la}} \qquad (6)$$

where I is nutrient influx (mol s^{-1} m^{-1}). Inserting Eq. 6 into Eq. 5 and some transformation yields:

$$I(t) = \frac{\overline{C_l}2\pi D_e b}{-\frac{1}{2} + \frac{r_s^2}{r_s^2 - a^2}\ln\left(\frac{r_s}{a}\right)} \qquad (7)$$

The single root approach originally assumes homogeneous distribution of the roots within a soil layer, i.e.

all of the catchment areas and the corresponding single root cylinders have equal size. In order to consider impact of heterogeneous root distribution, we followed Barley (1970) and assigned soil cylinders to each root of the Thiessen map (Fig. 1b), i.e. to a population of roots with different sizes of the Voronoi polygons. Therefore, the polygon area of a root was equated to the base area of a corresponding single root cylinder. It was assumed that the boundary of the base area is equivalent to the boundary of the Voronoi polygon. Nutrient uptake then is calculated separately for each root by use of Eq. 7.

Computational efficient versions of the one-dimensional single root model

In order to reduce computational effort we tried to diminish the number of single root cylinders to be calculated by defining representative cylinders from a distribution function. According to the literature, the frequency distribution of both the Voronoi polygons areas and root length density is mostly very skewed (Tardieu 1988a; van Rees et al. 1994). Observed frequencies of the area values can often be approximated by a lognormal distribution (Fig. 2a). The assumption of lognormal distribution was tested. Hence, values of the Voronoi polygon area were logarithmically transformed and Shapiro–Wilk W tests were then used to test these values for the normality of distribution (null hypothesis). Statistical significance for the test was set at $p \leq 0.05$. Statistical analysis was carried out with the R statistic system (R Development Core Team 2005).

Values of the mean μ and the standard deviation σ obtained from measured area distribution are used as input parameters for the one-dimensional model. A distribution function was then generated and classified. Class intervals were chosen in a manner that each class contains the same cumulative frequency. Specific area values for each class were obtained representing the area of a single root cylinder.

The curve shape of the probability density function within a class is often far from linearity. Therefore, the median may not be suitable to serve as a substitute of the area values occurring in a certain class (Fig. 2b).

In order to get suitable representative values each class was further divided into $n=10$ intervals. The area value of the interval j, ν_j (m^2), is calculated as:

$$\nu_j = B_1 + \frac{(B_u - B_1)}{n}(j - 0.5) \tag{8}$$

where B_u is the upper boundary, B_1 the lower boundary of area class i (m^2) and n is the number of intervals (–). Then the representative area for class i is calculated by:

$$A_{pi} = \sum_{j=1}^{n} \nu_j W_j \tag{9}$$

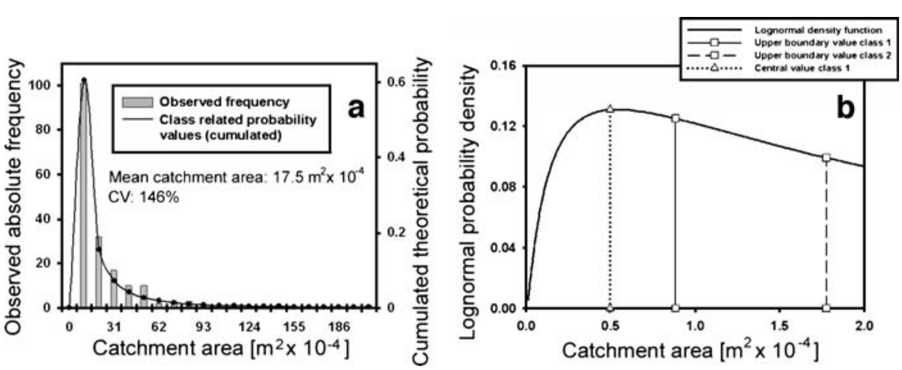

Fig. 2 **a** Observed absolute frequencies obtained from root distribution shown in Fig. 1 (72 DAS). Values are grouped into 20 classes with uniform class sizes. Cumulated probability values, which were derived from a lognormal probability density function, were presented for each class. **b** Detail view on the probability density function for the root distribution shown in Fig. 1 (*solid line*), divided into 10 classes. Both the upper boundaries of the 1st and the 2nd class and the median of the 1st class are presented

where A_{pi} is the representative polygon area of the i-th class (m^2), and W_j is a weighting factor (–), which is given by:

$$W_j = \frac{f(v_j)}{\sum_{j=1}^{n} f(v_j)} \tag{10}$$

where f is the probability density function.

Values of A_{pi} were used to calculate the corresponding radii of the single root cylinders r_s. Then, using Eq. 7 nitrate influx rate can then be quantified separately for each class and the nitrate influx rate of the entire system I_{tot} is given by:

$$I_{tot}(t) = \sum_{i=1}^{k} I_i(t) W_i \tag{11}$$

where I_i refers to nitrate influx rate of a certain class (mol s^{-1} m^{-1}), k is the number of classes (–) and W_i is a weighting factor (–). The term W_i is given by:

$$W_i = \frac{A_{pi}}{\sum_{i=1}^{k} A_{pi}} \tag{12}$$

Because classification may affect the results of the one-dimensional model, both model versions using a certain number of classes (10 and 20, referred to as 1D-10 and 1D-20, respectively) and a one-dimensional model that determines nitrate uptake individually for each root (referred to as 1D-R) were developed. For the latter one cumulative uptake was simply obtained by summation.

Two-dimensional approach

In this section, a simplification of the continuity equation is derived dealing with nutrient transport in two dimensions by means of diffusion. Two two-dimensional models ('2D' and '2D-S') designed for simulation of both nitrate transport and uptake are presented. They differ merely in calculating the sink term.

Regarding solute transport by diffusion in two dimensions one finds:

$$\frac{\partial(\theta C_l)}{\partial t} = -\frac{\partial}{\partial x}\left(D_e \theta \frac{\partial C_l}{\partial x}\right) - \frac{\partial}{\partial y}\left(D_e \theta \frac{\partial C_l}{\partial y}\right) - I(x,y,t)L_v(x,y,t) + P_m(x,y,t) \tag{13}$$

where L_v is root length density (km m^{-3}) and x, y are Cartesian coordinates in a plane (m).

The partial differential Eq. 13 was solved using the so-called ADI (alternating direction implicit) procedure (Douglas and Peaceman 1955; Douglas and Rachford 1956). In applying this concept, every time step is disassembled into two time segments. In the first one, implicit temporal integration is done for one spatial direction, in the second for the other. Within a time step Δt the change of nutrient content within a certain grid cell results from the differences of inflows and outflows from the two considered dimensions and the amount of nitrogen mineralised from soil organic matter and the uptake of nutrients by the plant roots. The average concentration of the solution in the soil is calculated from their arithmetic means.

The difference between the 2D and the 2D-S model refers to the calculation of nitrate uptake by the roots (Fig. 3).

In case of the 2D model, the nitrate influx rate I is calculated by (cf. Fig. 3a):

$$I(x,y,t) = D_e b\left(\frac{C_{(x-1,y)}}{\mathrm{dx}}\mathrm{dy} + \frac{C_{(x+1,y)}}{\mathrm{dx}}\mathrm{dy} + \frac{C_{(x,y-1)}}{\mathrm{dy}}\mathrm{dx} + \frac{C_{(x,y+1)}}{\mathrm{dy}}\mathrm{dx}\right) \tag{14}$$

where dx refers to the diffusion distance (mm) and dy is grid spacing (mm).

In case of the 2D-S model the concentration profile within the sink cell is calculated using the steady state approach as applied in the single root model. The nitrate influx rate I is calculated according to Eq. 7. Note that ($\overline{C_l}$) is given by the mean nitrate concentration of the sink cell and that r_s refers to the radius of the inscribed circle of the sink cell (Fig. 3b). At the beginning of the simulation initial concentration of solute in the liquid phase is uniform for all grid cells. For the outer boundary condition, it is assumed that there is no solute flux beyond the dimensions of the observed area.

Further assumptions

Soil heterogeneity is not considered by the models. Nevertheless, the models are designed to take changes in water content into account. However, for simplicity water content was not changed in this study. Neither age-related differences nor differences in the root radius were considered. The roots differ merely by

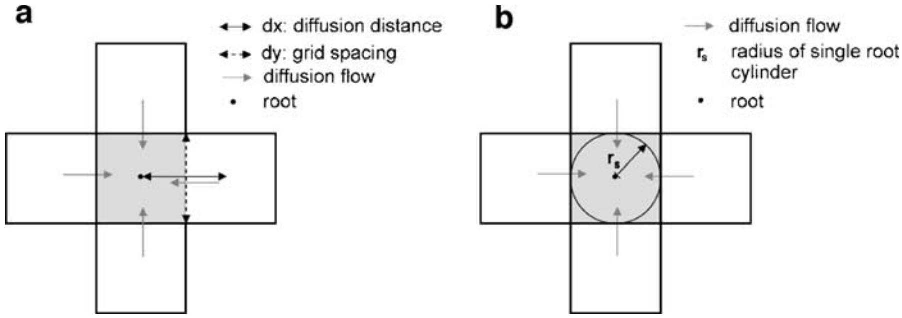

Fig. 3 Sketch exemplifying calculation of nitrate influx into a root for the 2D model (**a**) and the 2D-S model (**b**), respectively

their spatial position and – as a result – by the size of their catchment area.

Results

Observed root length densities and CV values

Root maps were used to get spatial coordinates and to derive aggregated parameter values for a distribution of summer barley roots in the subsoil (Fig. 1). Measured mean root length densities in the area between 0.35 and 0.8 m depth were 0.57 km m^{-3} for the early measurement date (72 DAS) and 1.29 km m^{-3} for the later one (86 DAS). The histogram of Voronoi polygon areas in the subsoil was extremely right-skewed. The areas of the Voronoi polygons showed clearly different coefficients of variation between the measurement dates. CV values for the early measurement were 146% and 250% for the later one.

Shapiro–Wilk tests indicated that a log normal distribution function fits the investigated root data quite well (W=0.9942 with a p value of 0.1108 for the root distribution measured at the 72nd DAS and by W=0.9916 with a p value of 0.1061 for the root distribution mapped at the 86th DAS, cf. Fig. 2a).

Effect of spatial resolution on simulated nitrate uptake

Impact of spatial resolution on the nitrate uptake rates was calculated by both the 2D and the 2D-S model. Therefore, the size of the grid cells was systematically altered. Moreover, percentage deviation between simulated nitrate uptake rates obtained at lower spatial resolution and at a high spatial resolution (2 mm grid spacing) was calculated as a measure for the impact of spatial resolution on the output of the two-dimensional models. Percentage deviation was used for comparison in case of both regular and irregular root distributions.

Since the single root approach may be regarded as exact in case of homogeneous root distribution, the 1D-R model was treated as a reference for evaluation of the two-dimensional models. The 1D-R model assumes steady state conditions, i.e. the depletion zone reaches the boundary of the single root cylinder instantaneously. For the purpose of comparison, it was necessary to consider the nitrate uptake rates that were calculated by the two-dimensional models after the steady state had established. Therefore, steady state was created by redistributing absorbed nitrate content evenly to each grid cell:

$$P_{\mathrm{m}i}(t) = \frac{\sum I(x,y,t)L_{\mathrm{v}}(x,y,t)}{n_{\mathrm{gc}}} \tag{15}$$

where $P_{\mathrm{m}i}$ refers to mineralisation rate in grid cell i, and n_{gc} is the number of grid cells (–). Parameter values used for the models are given in Table 1.

Even in case of a regular root distribution, the 2D model computed much higher nitrate uptake rates than the 1D-R model. This holds for all spatial resolutions used (Fig. 4a). Simulated nitrate uptake rates at steady state decreased almost linearly with increasing spatial resolution (Fig. 5a). Even using a quite high spatial resolution (2 mm grid spacing), the nitrate uptake rate predicted by the 2D model was 28% higher than the value of the 1D-R model. Nitrate uptake rates calculated by the 2D-S model for regular root distribution, however, were very similar to the results obtained from the 1D-R model (Fig. 4b).

With higher root length densities the 2D model was more sensitive to an altered spatial resolution (Fig. 5a). In contrast to these results, simulated nitrate uptake rates of the 2D-S model were not significantly influenced by changing the spatial resolution. Percentage deviation of results, which were obtained at lower spatial resolution, in comparison to the output at 2 mm grid spacing was less than 1.5% for all cases tested (Fig. 5a).

Table 1 Parameter values used in the calculations for both evaluating the impact of the spatial resolution on the results of the 2D and the 2D-S model and for comparison of the 2D-S and the one-dimensional single root model

Symbol/definition	Value	Units	Reference
θ (soil moisture fraction by volume)	0.18	m^3 m^{-3}	
a (radius of root axis)	0.2×10^{-3}	m	
D_l (diffusion coefficient of solute in water)	1.92×10^{-9}	m^2 s^{-1}	Barraclough (1989)
Size of layer	0.3	m	
Initial N content in the considered layer (0.3 m)	30	kg N ha^{-1}	

In case of an irregular root distribution, the 2D model is again much more sensitive to a modified spatial resolution compared to the 2D-S model (Fig. 5b). Nevertheless, for the irregular root distributions tested, the spatial resolution has distinct impact on the output of the 2D-S model as well (Fig. 5b). However, the difference of nitrate uptake rates simulated by the 2D-S model was less pronounced at higher spatial resolutions. Results obtained at 3.3 mm grid spacing differ solely 1.1% from the result achieved at 2 mm grid spacing (Fig. 5b).

At the beginning of simulation both the 2D and the 2D-S model are in transient state, i.e. a certain time is required for successive approximation to steady state conditions (Fig. 4). This may cause differences between calculation methods considering or neglecting transient state effects. During transient state, the concentration distribution within the catchment area of a root is changing even for our approach to induce a steady state situation for the 2D and 2D-S model by redistributing nitrate uptake evenly between all cells of our domain (Fig. 6). At the beginning of the simulation, the 2D-S model calculated quite steep nitrate concentration gradients near the root surface. At runtime, the results of the 2D-S model approximated the concentration profile at steady state, which was predicted by the single root model. In the example given, steady state was reached after a relatively short period (Fig. 6). After 10 days of simulation time, the calculated nitrate uptake rate differed less than 7% from the results obtained by the single root model (Fig. 4b).

The period of the transient state increased, if root length density decreased or CV values increased. Regarding root distribution measured at the 72nd DAS (L_v=0.57 km m^{-3}, CV=146%), for example, nitrate uptake rate calculated after 40 days was still approximately 45% higher than the nitrate uptake rate simulated at steady state (data not shown).

At the end of transient state, a constant distribution of nitrate concentrations develops in the soil, which clearly depends on different root distributions (Fig. 7).

Effect of concentration profiles near the root surface on calculated nitrate uptake rates

The concentration profile with subject to spatial resolution was examined for both the 2D and the 2D-S model within the catchment area of a root in order to further analyse causes for differences in nitrate uptake rates (Fig. 8).

Differences in the modelled nitrate concentration value in the sink cell between the two dimensional models were striking. In case of the 2D model, nitrate concentration in the sink cell was zero according to Eq. 14. Corresponding mean nitrate concentration in

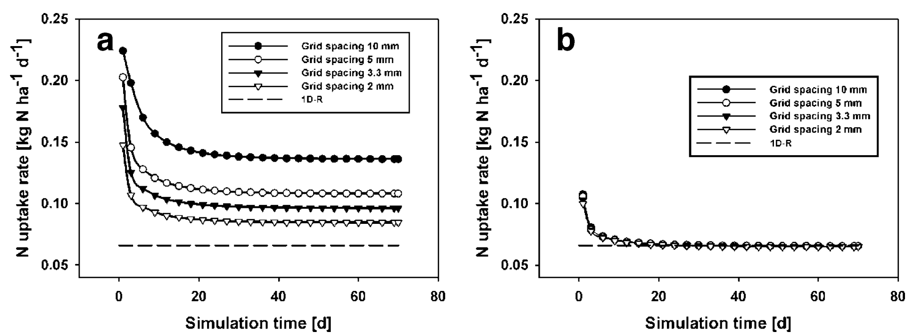

Fig. 4 Time course of simulated nitrate uptake rates for different spatial resolutions given by the 2D model (**a**) and the 2D-S model (**b**). Nitrate uptake rate simulated by the 1D-R model is presented (*dashed line*). A regular root distribution (L_v=0.1 km m^{-3}) was used

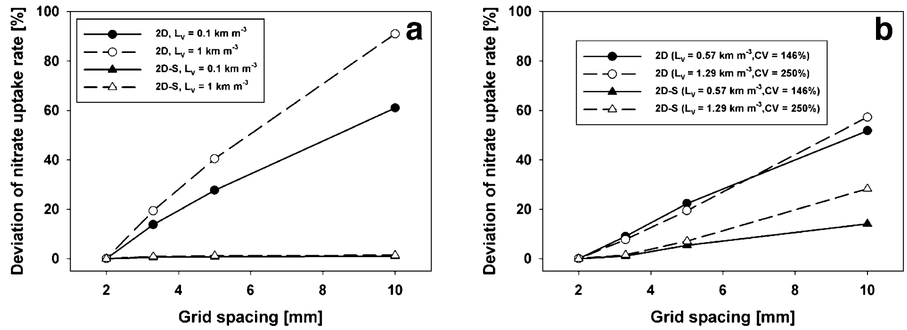

Fig. 5 Percentage deviation of the simulated nitrate uptake rate in relation to a fixed comparison value for both regular (**a**) and irregular (**b**) root distributions when both root length density and coefficient of variation are considered. Reference value was nitrate uptake rate calculated using 2 mm grid spacing

the sink cells of the 2D-S model was very much higher (Fig. 8).

In the immediate vicinity of the root, the 2D model simulated lower nitrate concentrations with lower spatial resolution. Simulated nitrate concentrations in this region were generally below the values of the single root model. At greater distance from the root surface, spatial resolution had only slight effects on the concentration profile. The simulated nitrate concentration was even a little higher for 10 mm grid spacing than for all other spatial resolutions investigated. A relatively good approximation to the results of the single root model was obtained by the use of a very high spatial resolution (2 mm grid spacing) only.

The 2D-S model calculated nitrate concentrations that were very similar to the results of the single root model even when coarser spatial resolution was applied. In contrast to the 2D model, the concentration profile obtained by the 2D-S model lay slightly above the profile given by single root model with the exception of a small region near the boundary of the catchment area (Fig. 8b).

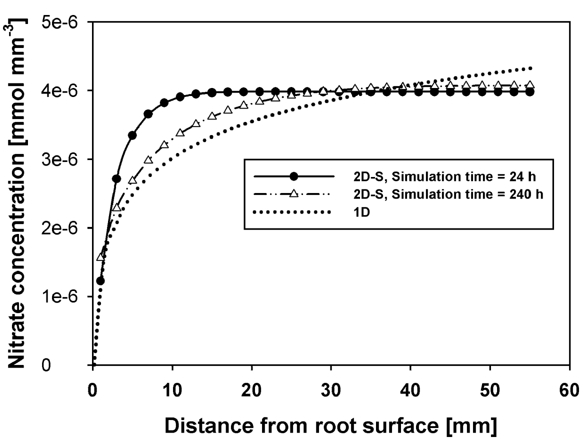

Fig. 6 Simulated concentration profiles in the vicinity of the root obtained from the 2D-S model after 24 and 240 h simulation time, respectively. A regular root distribution (L_v= 0.1 km m^{-3}) was used. Concentration profile given by the single root model is also presented (*dotted line*)

Comparison of the one-dimensional single root model with the 2D-S model in case of heterogeneous root distribution

In case of heterogeneous root distribution, both the geometry of the Voronoi polygons may become irregularly shaped and the root may be located eccentrically within the polygon. Diffusion distances within the polygon may then clearly differ from the uniform diffusion distances within a circular single root cylinder. Under these conditions, diffusion flows can probably not be described accurately by use of the single root approach anymore. Hence, the 2D-S model, which was successfully tested for modelling nitrate uptake for regular distribution, was used as a reference for evaluation of all one-dimensional models in case of heterogeneous root distribution. The one dimensional single root approach if leading to sufficiently correct results may have a higher computational efficiency than the 2D-S model.

Nitrate content in soil calculated both by the 2D-S model and the 1D-R model agreed well (Fig. 9a). For low L_v values heterogeneous root distribution showed pronounced influence on simulated nitrate amount in the soil and therefore on nitrate uptake by roots. After 90 days of simulation, nitrate content in the soil was much lower for a regular root distribution than for an irregular root distribution with a corresponding L_v value and a CV value of 146% (Fig. 9a).

Both the 1D-R model and the model versions using classification (1D-10, 1D-20) calculated nitrate amounts in soil, which were very close with the results given by the 2D-S model (Fig. 9b). There were

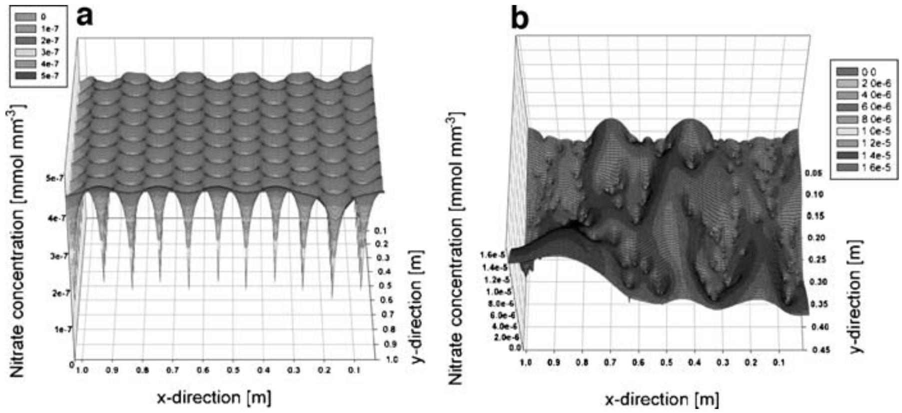

Fig. 7 Examples of simulated nitrate concentration in the soil with respect to different root distributions calculated by the 2D-S model at steady state for a regular root distribution (L_v=0.1 km m^{-3}) (**a**) and the irregular root distribution (**b**) shown in Fig. 1. Note that the *z*-axis does not refer to depth but to nitrate concentration in the soil

no substantial differences between the 1D-10 and the 1D-20 models.

Discussion

Different approaches, which allow the simulation of nitrate transport and uptake by an irregular distributed root system, were compared. Therefore, both one-dimensional and two-dimensional models were developed. The two-dimensional models differ merely in calculating the sink term, i.e. the uptake rates of nitrate within cells containing roots. Classification was applied to the one-dimensional model in order to reduce computing time and memory requirements.

The ability of the different modelling approaches to accurately describe effects of heterogeneous root distribution will be analyzed and the results are related to similar existing models. Furthermore, applicability of the model approaches described is discussed.

Relevance of heterogeneous root distribution

Results given by the literature concerning the influence of non-regular root distribution on nutrient uptake are not consistent. Barley (1970) reported that nutrient uptake was little affected by heterogeneous root distribution. It should be emphasized that a highly clustered root distribution was not considered in this work. In contrast, some modelling studies (Baldwin et al. 1972; Comerford et al. 1994; de Willigen and van Noordwijk 1987a) suggest that irregular root distribution patterns may have considerable effect on nutrient acquisition by plants. However, not only CV values, but also actual root length densities and the value for D_e need to be considered. Therefore, the conclusion can be made that cereals, in general, can exhaust available nitrate in the soil even in case of moderately low root length densities. Nevertheless, nitrate uptake of cereals may be limited by solute transport if markedly low root length densities or high CV values (Kage 1997) occur.

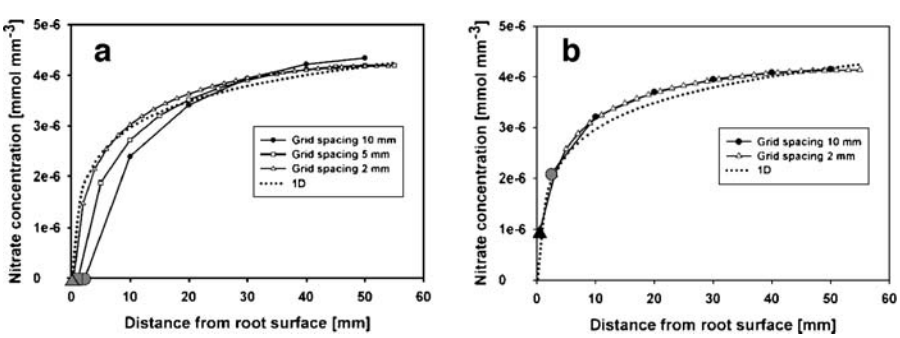

Fig. 8 Influence of spatial resolution on simulated nitrate concentration near the root surface given at steady state for the 2D model (**a**) and the 2D-S model (**b**). Concentration profile calculated with the single root model is presented (*dotted line*). In **b**, the concentration profile was shown only for grid spacing of 10 mm and 2 mm, respectively. A regular root distribution (L_v=0.1 km m^{-3}) was used. *Grey symbols* indicate mean concentration values in the sink cell

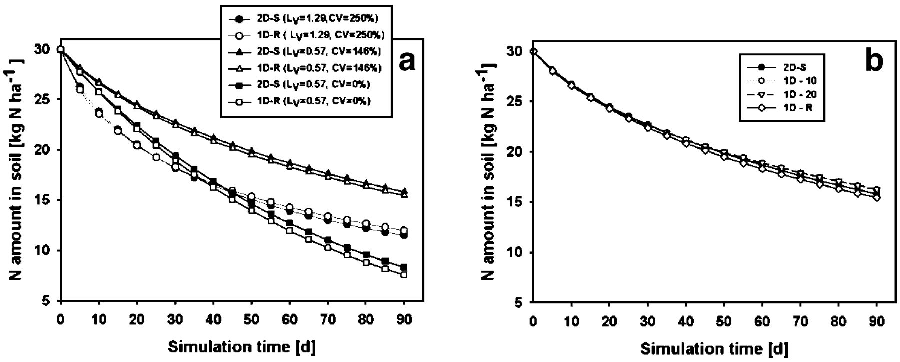

Fig. 9 **a** Time courses of simulated N amount in a soil layer of 0.3 m for different root distribution patterns measured in the subsoil calculated by the 2D-S model and the 1D-R model. Results obtained for a regular root distribution are also presented. **b** Time courses of simulated nitrate amount for an irregular root distribution (L_v=0.57 km m^{-3}, CV=146%) calculated by the 2D-S model and the 1D-R, 1D-10 and 1D-20 models, respectively

Since both factors were associated, transport-limiting conditions in case of cereals most likely may occur at the beginning of plant development or in the subsoil. This is confirmed by the results of our study. Both the 2D-S model and the one-dimensional models showed clear effects of heterogeneous root distribution on nitrate uptake in the subsoil (Fig. 9a).

Barraclough (1986) simulated the nitrate concentration in the bulk soil that was necessary to maintain high nitrate influx. Calculated threshold concentration in this study was always lower than 1.7×10^{-7} mmol mm^{-3} and therefore much lower than the results obtained from our simulation (Figs. 6 and 8). Barraclough acquired data for his model from winter wheat and for a given nitrate inflow. By contrast, our work focuses on the calculation of maximum transport limited uptake rates of parts of a root system. Thereby we assume that this situation is relevant for the subsoil and a crop with low root density values.

Under these specific conditions, the assumption of a concentration at root surface close to zero is justified even for considerably higher nitrate concentrations in the bulk soil.

One-dimensional single root models

Within the single root cylinder, the single root approach presumed a uniform steady state concentration profile, which was established instantaneously.

In case of heterogeneous root distribution, the concentration profile may differ substantially from this assumption. This is indicated by both the irregular shape of the Voronoi polygon and the eccentric position of the roots. Therefore, the geometric properties of an irregular root system may lead to inaccurate results given by the single root models (1D-R, 1D-10, 1D-20).

Moreover, the steady state approximation does not account for additional nitrate uptake by the roots during the transient state. This suggests, that nitrate uptake at the beginning of simulation will be underestimated by the one-dimensional model.

However, the one-dimensional models showed only small deviation from the results obtained by the 2D-S model even if root distribution was highly clustered (Fig. 9).

De Willigen and van Noordwijk (1987b) found that both an eccentric position of the root and an irregular geometry of the Voronoi polygon are less important for mobile nutrients, such as nitrate. This was confirmed by the results of our study. Yanai (1994) found that additional nutrient uptake during transient state strongly depends on D_e. For mobile ions, such as nitrate, transient state may be less important and its contribution to total uptake may be negligible.

Since the results of the 1D-10 and the 1D-20 model were very close with the results given by the 1D-R model, the presented approach for classification is appropriate to simulate nitrate uptake of an irregular distributed root system.

Two-dimensional models

Our results clearly indicate that the results obtained by the 2D model very much depend on the spatial resolution used even for a regular root distribution. This was caused by calculating nitrate uptake due to a supposed linear concentration gradient between the centre of the sink cell and the centres of its adjacent neighbours (Eq. 14). In fact, concentration gradients in the vicinity of the root surface are in most cases far from linearity (Fig. 8). Moreover, the 2D model does not calculate uptake subject to the root surface but to the edges dy of the grid cells (Eq. 14). Consequently, nitrate uptake was overestimated (Fig. 4a).

The 2D model therefore required a very high spatial resolution in order to establish concentration profiles, which corresponded roughly to those obtained by the 1D model.

In contrast, the 2D-S model uses the single root approach to simulate the concentration profile within the sink cell, i.e. in the immediate vicinity of the root surface. Nitrate uptake at root surface was calculated in dependence on the mean nitrate concentration within the sink cell (Eq. 8). As a result, both uptake rates and the nitrate concentration profile within the catchment area simulated by the 2D-S model were quite similar to the results given by the 1D model. This was valid even for a low spatial resolution (Figs. 4b and 8b).

However, if applied to a heterogeneously distributed root system the 2D-S model showed distinct impact of spatial resolution on nitrate uptake rates. Since inter-root distance of a highly clustered root system was very low in certain regions, it is still necessary to apply a high spatial resolution to achieve a minimum number of grid cells between two adjacent roots and a sufficient approximation of the concentration profile between them.

The findings of our study indicate that the spatial resolution that was frequently used by existing multidimensional models may sometimes be insufficient for correct calculation of the effects of heterogeneous root distribution on the uptake of root systems. This holds in particular for highly clustered root systems or for simulation on a crop scale.

In the model of Somma et al. (1998), the finite element size was usually set within a centimetre range. The SERMUN model (Craine 2006; Craine et al. 2005) in contrary, uses a very fine-scaled grid of voxels. Each voxel represents a volume of 0.0004 mm^3. However, the model was limited to a 100×100 square grid and used a purely implicit technique to calculate nutrient fluxes between adjacent cells. Therefore, SERMUN was restricted to surveys on a smaller spatial and temporal scale.

The model of Vrugt et al. (2001a, b) uses the HYDRUS-2D flow code (Šimunek et al. 1999) for simulation of transient water flow in two dimensions. However, it does not use a mechanistic description of root uptake but an empirical, exponential model of root water uptake.

A few existing models, which joined solute transport and uptake by roots, use the single root approach in a similar manner to the 2D-S model (Benjamin et al. 1996; Dunbabin et al. 2002a).

Dunbabin presented a model of root growth and nutrient uptake, which was mostly applied for lupins, i.e., for a rather sparsely dense root system (Dunbabin et al. 2002a, b, 2003, 2004). It was used, however, in a simulation study with wheat (Dunbabin et al. 2006). Reliability of the model output was tested on the rhizosphere scale and for an individual root segment. Integration of the single root approach may reduce errors caused by inadequate spatial resolution. However, the findings of our study suggest that it was necessary to consider the effects of spatial resolution in line with any up-scaling process. This holds particularly for the dense and highly clustered root system of cereals.

Genuine finite element models, which take advantage of adaptive discretization, are seldom used. The model of Bruckler et al. (2004) is an exception. However, this model does not account for a dynamically growing root system.

Therefore, development of a finite element model, which supports adjustment of the finite element mesh to a dynamically growing root system and the integration of the single root model into the sink elements, may be desirable for surveys carried out on a crop scale.

Application of the models

The 2D-S and the one-dimensional models yielded very similar simulation results for nitrate uptake of a fixed and heterogeneously distributed root system. With respect of modelling the dynamics of a growing root system, however, the models may differ in their applicability.

Basically, it is possible to use the single root approach for modelling nitrate uptake of a growing root system. This was mostly done for a regular distribution of the root system (Nye et al. 1975; Yanai 1994). These models usually calculate nutrient uptake depending on the average nutrient concentration in the bulk soil and a changing radius of the single root cylinder, which was both readjusted for each time step.

Description of nutrient uptake considering dynamic growth of a heterogeneously distributed root system is rather difficult, since dynamic changes also occur in nutrient concentration of the bulk solution.

Because nutrient concentration within any grid cell was calculated for each time step and the position of newly developed roots is known, the two-dimensional model may be well suited to represent dynamic uptake of a growing root system.

Two-dimensional models are furthermore indispensable for a number of applications such as investigations of the impact of soil heterogeneity on plant uptake (e.g. local variability of water content in drip irrigated agricultural systems or effects caused by wheel compaction). Moreover, heterogeneous root system patterns may affect movement of water and nutrients on a larger scale. This holds particularly for widely spaced crops, where plant uptake may cause higher nutrient or water content in some distance from the row. A higher downward movement of nutrient may then occur from these regions especially in case of mobile ions, such as nitrate. Such a modelling scheme needs at least the coupling of a water transport and an uptake model considering water transport of small and larger scales. The 2D-S model is likely better adapted than the one-dimensional models to meet these requirements.

Conclusion

The single root approach was applied to 'sink cells' of a two-dimensional nitrate transport and uptake model. It was shown that this approach might be an important improvement in order to reduce requirements for high spatial resolution. However, for modelling nitrate uptake of a heterogeneous root system a sufficient number of grid cells is still necessary.

Keeping specific restrictions in mind a two-dimensional model can be substituted by a one dimensional single root model. The one-dimensional model is particularly able to simulate nitrate uptake of a static root system irrespective whether a root system is irregularly distributed or not.

Regarding a dynamically growing root system or considering impact of local soil properties on root growth and uptake, a two-dimensional modelling approach is likely to be indispensable.

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Appendix

List of the used main symbols

Symbol	Definition	Units
a	Radius of root axis	m
A_{pi}	Representative polygon area of the i-th class	m^2
B_l	Lower boundary of the i-th area class	m^2
B_u	Upper boundary of the i-th area class	m^2
b	Buffering	–
C_i	Initial concentration of solute in liquid phase	mol m^{-3}
C_{la}	Concentration of solute at root surface	mol m^{-3}
C_l	Concentration of solute in liquid phase	mol m^{-3}
$\overline{C}_l$	average concentration of solute in liquid phase	mol m^{-3}
D_l	Diffusion coefficient of solute in water	$m^2\ s^{-1}$
D_e	Effective diffusion coefficient (diffusion coefficient of solute in soil)	$m^2\ s^{-1}$
dx	grid width in x direction and diffusion distance, respectively	mm
dy	grid width in y direction	mm
f	Impedance factor	–
k	Number of used classes	–
L_v	Mean root length density	km m^{-3}
I	Nutrient influx rate per root length unit	mol s^{-1} m^{-1}
I_i	Nutrient influx rate of the i-th class	mol s^{-1} m^{-1}
I_{tot}	Weighted nutrient influx rate of all classes	mol s^{-1} m^{-1}
n	Number of used intervals	–
n_{gc}	Number of grid cells	–
P_m	Mineralisation rate	mol s^{-1} m^{-3}
P_{mi}	Mineralisation rate of grid cell i	mol s^{-1} m^{-3}
r	Radial coordinate	m
r_s	radius of the single root cylinder	m
t	Time	s
W_i, W_j	Weighting factors	–
x, y	Cartesian coordinates in two-dimensional space	m
α	Root absorbing power	m s^{-1}
ν_j	Area of the j-th interval	m^2
θ	Soil moisture fraction by volume	$m^3\ m^{-3}$

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