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REGULAR ARTICLE

Modelling diverse root density dynamics and deep nitrogen uptake—A simple approach

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Abstract We present a 2-D model for simulation of root density and plant nitrogen (N) uptake for crops grown in agricultural systems, based on a modification of the root density equation originally proposed by Gerwitz and Page in J Appl Ecol 11:773–781, (1974). A root system form parameter was introduced to describe the distribution of root length vertically and horizontally in the soil profile. The form parameter can vary from 0 where root density is evenly distributed through the soil profile, to 8 where practically all roots are found near the surface. The root model has other components describing root features, such as specific root length and plant N uptake kinetics. The same approach is used to distribute root length horizontally, allowing simulation of root growth and plant N uptake in row crops. The rooting depth penetration rate and depth distribution of root density were found to be the most important parameters controlling crop N uptake from deeper soil layers. The validity of the root distribution model was tested with field data for white cabbage, red beet, and leek. The model was able to simulate very different root distributions, but it was not able to simulate increasing root density with depth as seen in the experimental results for white cabbage. The model was able to simulate N depletion in different soil layers in two field studies. One included vegetable crops with very different rooting depths and the other compared effects of spring wheat and winter wheat. In both experiments variation in spring soil N availability and depth distribution was varied by the use of cover crops. This shows the model sensitivity to the form parameter value and the ability of the model to reproduce N depletion in soil layers. This work shows that the relatively simple root model developed, driven by degree days and simulated crop growth, can be used to simulate crop soil N uptake and depletion appropriately in low N input crop production systems, with a requirement of few measured parameters.

Keywords EU_rotateN · Vegetable crops · Root depth · Root distribution · Root model · Wheat

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Introduction

Plant and soil models are commonly used to predict crop yield and the environmental impact of crop production. Such models often combine complex modelling of water movement, soil organic matter turnover and aboveground plant growth. Simulation of root growth is an important part, because roots are the link between mineral N in soil and plant N. Good models of crop root growth are important to simulate N use efficiency within rotations (Delgado et al. 2000).

While the simulation of aboveground plant growth has become increasingly advanced over the years, root modelling has remained fairly simple due to the lack of field data to calibrate more sophisticated root models at field scale. Some root models including detailed modelling of individual roots have been developed (Kohl et al. 2007; Pages et al. 2004). However, such models are mainly used for scientific work and are generally not suitable for simulation of real crop rotations because of a lack of input data and because the models are often only developed for one or a few plant species.

Recent field studies have shown that the development of crop rooting depth can be described by a lag phase starting at sowing or transplanting, after which root depth increases linearly with temperature sum (Kage et al. 2000; Smit and Zuin 1996; Thorup-Kristensen and Van den Boogaard 1998).

Rooting depth and root architecture differ significantly between crop species (Kutschera 1960). For monocot species, root penetration rates in the range of about 0.2 mm day-degree^{-1} have been observed for onion (Thorup-Kristensen 2006a) and 0.8 to 1.2 mm day-degree^{-1} for cereals and grasses (Thorup-Kristensen 2001). For dicot species, penetration rates are about 0.7 mm day-degree^{-1} for carrot (Thorup-Kristensen and Van den Boogaard 1999) and between 1.2 and 2.5 cm day-degree^{-1} or even higher for white cabbage and fodder radish (Smit and Groenwold 2005; Thorup-Kristensen 2001). Final rooting depth is related to penetration rate and length of growing season. Thus onions develop only a very shallow root system down to approximately 0.2 to 0.3 m (Burns 1980; Thorup-Kristensen 2006a), ryegrass roots grow to approximately 1 m while white cabbage, red beet and fodder radish can grow to 2 m or more (Thorup-Kristensen 2006b).

Monocots and some dicot species have their highest root length densities near the surface, as observed in winter wheat (Asseng et al. 1997; Xue et al. 2003; Zuo et al. 2006), grasses (Smit and Groenwold 2005; Thorup-Kristensen 2001) and cauliflower and spinach (Kage et al. 2000; Smit and Groenwold 2005). However, many dicot species have a more uniform distribution of root length density in the soil profile, often with higher root densities in deeper soil layers than monocot species, as found e.g. for oilseed rape (Barraclough 1989) and fodder radish (Smit and Groenwold 2005; Thorup-Kristensen 2006b). For crops grown as row crops, e.g. maize and many vegetable species, a significant difference in root density below and between rows has been shown for maize (Liedgens and Richner 2001), onion and carrot (Thorup-Kristensen 2006a; Thorup-Kristensen and van den Boogaard 1999), whereas lettuce and white cabbage typically show the same root density below and between rows already during their early growth (Thorup-Kristensen 2006a).

The development and proliferation of the roots in soil are affected by intrinsic and extrinsic parameters such as the supply of photosynthates from the shoot, the nutrient status of the plant, soil type and compaction, water potential at the root surface and availability and distribution of nutrients (Bloom et al. 2003; Forde and Lorenzo 2001). Root penetration rate in root models is often described as being affected by air or soil temperature and a plant-specific growth rate coefficient. The daily growth rate is associated with water stress, soil compaction, clay or sand content and aeration (Penning de Vries et al. 1989).

A number of one-dimensional (1-D) models have been developed for modelling the soil-plant system to enable prediction of plant production, water and nitrogen dynamics in agricultural systems. In 1-D models, the soil column is divided into layers from the surface to a defined depth. Each layer can be assigned standard or specific parameters such as nutrient concentration, water content, temperature, bulk density, or soil strength. As 1-D models only distribute roots according to depth, this prevents them from taking into consideration the uneven root distribution of row crops. Two-dimensional (2-D) and three-dimensional (3-D) root models, on the other hand, are able to simulate spatial differences in nutrient uptake and root distribution of row crops, which leads to much more complex soil water and N dynamics.

Gerwitz and Page (1974) introduced a logarithmic function for root density calculations in 1-D systems. The function gives the percentage of roots for a given rooting depth, with the highest root density near the soil surface. The function has been modified and used in the Daisy model by Abrahamsen and Hansen (2000). Here root density is set to a very low default value at the bottom of the rooting zone, so a very low root density will always be simulated close to the rooting depth; variations in total root length have little effect on subsoil root length and nearly all variation is confined to the surface soil layers. This approach to root modelling prevents the model from simulating the relatively high root densities sometimes observed in deeper soil layers. Further, rooting depth in the model means absolute rooting depth, whereas the measured rooting depths used for parameterization normally does not. In the experimental data roots are also present below the observed rooting depth, and by using these values as estimates of absolute rooting depth in the model, the simulated root exploration of the subsoil will be less efficient than actually indicated by experimental results.

In this work we present a model for root growth and proliferation of root length density in the soil profile, assess whether this model is able to simulate a range of crop root systems, their N uptake and their soil mineral N depletion, and compare these against experimental field data. The purpose of this root model is to model a variety of arable and vegetable crop species and reproduce results from field experiments for soil mineral N depletion with a simple root modelling approach and a minimum of parameters and input requirements.

The objective of the present work was to test the ability of the newly developed root model to simulate root development and N depletion in the soil profile as known from the literature, and to compare simulated soil mineral N depletion against field observations for cereal and vegetable crops with different root patterns. The model was tested with respect to its: a) ability to simulate rooting depth and partitioning of root length density in the rooted zone, b) sensitivity of plant N uptake to parameter values determining root distribution, root growth and root system N uptake efficiency, and c) ability to simulate root development and plant N uptake in field crops.

Materials and methods

Plant and soil modules

The root model operates as a module in an integrated soil-plant-atmosphere model. In brief, other modules in the model include an aboveground crop development and N demand module (Greenwood et al. 1996; Greenwood et al. 2001), a soil organic matter, soil microbial biomass and decomposition of added organic matter module from the Daisy model (Hansen et al. 1991) and a water balance module (Brisson et al. 2003). While the root model simulate N uptake processes, the other soil N processes such as N mineralization, immobilization, denitrification and ammonia volatilization are modelled as described by Hansen et al. (1991).

The model runs on a daily basis. The information fed into the root module from other modules includes soil water content, ammonium and nitrate concentrations, root biomass increment and crop potential water and N demand, together with the weather data, soil clay content and bulk density from the model run setup files. All processes are calculated in 0.05 m× 0.05 m grid units within the soil domain of 2 m depth vertically and half the row width horizontally. Root density is calculated in 0.05×0.05 m soil units, up to 1 m horizontally (controlled by row width) and to 2 m depth vertically, and when root depth or width enters the centre of a new soil unit, root density is calculated and plant N uptake occurs. For crops planted more spatially homogeneously (row width < 0.1 m), the model operates in 1-D and only one soil column with 0.05 m width is considered.

Root module—1-D model

Root penetration

Root growth calculation is based on cumulative day-degrees (DD, Eq. 1), which is common for root models (Kage et al. 2000) and has been shown in field trials to be applicable to both monocot and dicot crops (Kirkegaard and Lilley 2007; Smit and Groenwold 2005).

$$DD = \sum T = \left\{ \begin{array}{ll} 0 & ; T_{\min} \geq T_{\mathrm{air}} \\ T_{\mathrm{air}} - T_{\min} & ; T_{\min} \leq T_{\mathrm{air}} < T_{\max} \\ T_{\max} - T_{\min} & ; T_{\mathrm{air}} \geq T_{\max} \end{array} \right\} \tag{1}$$

A lag phase (DD_{lag}) in terms of DD is set to account for the period from seed germination or transplanting to root penetration. The root penetration depth (R_z) is calculated as follows. Explanations of abbreviations used in the equations are shown in Table 1.

$$R_z = \left\{ \begin{array}{ll} \mathrm{R}_{z-\min} & ; \sum DD \le DD_{\mathrm{lag}} \\ \sum \left(\left(DD - DD_{\mathrm{lag}} \right) k_{rz} \right) + \mathrm{R}_{z-\min} & ; \sum DD > DD_{\mathrm{lag}} \\ R_{z-\max} & ; \sum \left(DD - DD_{\mathrm{lag}} \right) k_{rz} + \mathrm{R}_{z-\min} > R_{z-\max} \end{array} \right\} \quad (2)$$

The calculation of root penetration in the horizontal direction is similar to Eq. (2), and the calculation is restricted to the current rooting depth. The initial root system starts with the root depth 0.1 m and begins to grow horizontally and vertically after the DD_{lag}. The model calculates the root penetration depth until 2 m. $\mathrm{R}_{\text{z-max}}$ is default 2 m and can be adjusted in the setup file for soil information.

Root density

The total root length (L_r) is calculated from root biomass (W_r) by assuming a specific root length (S_r) (Eq. 3). The equation for root density distribution is a modified form of the equation suggested by Gerwitz and Page (1974). In the present version, the root density declines by a logarithmic function down to the simulated rooting depth R_z, while below R_z it decreases linearly to zero at q=1.3 (Eq. 4).

$$L_r = W_r S_r \quad (3)$$

$$L_z = \left\{ \begin{array}{ll} L_0 e^{(-a_z z)} & ; z < R_z \\ L_0 e^{(-a_z R_z)} \left(1 - \frac{z - R_z}{q R_z - R_z} \right) & ; q\mathrm{R}_z > z > R_z \\ 0 & ; z > q R_z \end{array} \right\} \quad (4)$$

Plant N uptake

Assuming a uniform distribution of roots in a soil unit, the potential nitrate and ammonium uptake in each unit is calculated by modifying the equation from Nielsen and Barber (1978) with root length as shown in Eq. 5.

$$N_{\mathrm{pot}}(i,j) = \frac{L_r k N (c - c_{\min})}{kf + c} \quad (5)$$

The calculations for nitrate and ammonium uptake are similar, but they are calculated separately for each unit and accumulated for the whole soil profile. Ammonium only appears in the first 6 soil layers (0–0.30 m) in the model.

Actual plant N uptake is calculated from the potential N uptake accumulated for the whole rooted zone and the plant N demand which comes as external information from the crop module. Eq. 6 shows the calculation of actual plant N uptake.

$$\mathrm{N}_{\mathrm{up}} = \mathrm{N}_{\mathrm{demand}} \left(1 - \mathrm{e}^{-1 \frac{\mathrm{N}_{\mathrm{pot}}(\mathrm{NO}_3^-) + \mathrm{N}_{\mathrm{pot}}(\mathrm{NH}_4^+)}{\mathrm{N}_{\mathrm{demand}}}} \right) \quad (6)$$

2-D root system

In the 2-D model the soil domain is divided into a 0.05 m×0.05 m grid. If a row crop has a row width greater than 0.1 m, the root module calculates root density in 2-D. The default root model assumes the same penetration rate in both directions, but different form parameters (a_z and a_x) are used for vertical and horizontal root density distribution. Horizontal growth stops in the middle of the inter-row, and competition between crop rows is not allowed in this model.

Model simulations

For testing the significance of parameter values, model simulations were run for 110 days starting from 1 April, with typical Danish weather conditions averaged for the period 1960–1990. Precipitation/irrigation was set according to evapotranspiration, to ensure a minimum downward percolation of nitrate during the crop growth period. Soil texture was selected so that it did not restrict the root penetration rate and root distribution. The default parameter

Table 1 List of abbreviations, initial value if needed, units and explanation

Name	Default value	Unit	Explanation
Model parameters			
a_z	[0,1..8]	–	Form parameter, vertically
a_x	[0,1..8]	–	Form parameter, horizontally
c	–	[kg N m^{-3}]	Nitrate or ammonium content in soil unit
$cmin$	0.001 / 0.002	[kg N m^{-3}]	Minimum nitrate / ammonium concentration allowing N uptake from a soil unit
kf	1.45	–	Parameter reducing root N uptake at low N concentrations
kN	0.07	–	Root N uptake efficiency parameter
k_{rz}	–	[m day^{-1} °C^{-1}]	Vertical root penetration rate parameter
q	1.3	–	Absolute rooting depth relative to simulated rooting depth
R_x	–	[m]	Root system width
R_z	–	[m]	Vertical root depth
R_{z-max}	–	[m]	Maximum rooting depth
R_{z-min}	0.10	[m]	Rooting depth at sowing or planting
S_r	300,000	[m g^{-1}]	Specific root length
T_{min}		[°C]	Minimum temperature for root growth
T_{max}	T_{min}+20	[°C]	Maximum temperature for root growth
DD	–	–	Day-degrees
DD_{lag}	–	[DD]	Lag phase for initiating root growth
T	–	[°C]	Temperature
L_0	–	[m m^{-3}]	Root density at surface
L_r	–	[m m^{-2}]	Total root length
L_z	–	[m m^{-3}]	Root density at soil depth z
N_{demand}	–	[kg N ha^{-1}]	Nitrogen demand calculated
$N_{pot}(i,j)$	–	[kg N]	Potential nitrate or ammonium N uptake for each soil unit (i,j), where i denotes depth and j denotes width
N_{pot}	–	[kg N ha^{-1}]	Potential daily N uptake from the whole root zone
N_{up}	–	[kg N ha^{-1}]	Actual nitrate and ammonium plant uptake
W_r	–	[g m^{-2}]	Root biomass
z	–	[m]	Soil depth

values in the root module are shown in Table 1 and the method was tested with form parameter value a_z ranging from 0 to 8. Potential crop N demand in the model corresponded to 250 kg N ha^{-1} and simulations were carried out for both soil mineral N contents below and above sufficient supply for this demand. For the low soil N conditions, 70 and 32 kg mineral N ha^{-1} were distributed in the 0–1 and 1–2 m depth, respectively. For the high soil N conditions, 415 and 185 kg mineral N ha^{-1} were distributed in the 0–1 and 1–2 m depth, respectively. The effects of root penetration rate k_{rz}, and plant N uptake efficiency kN were also studied. To do so, the model was run with settings of k_{rz}=90% of default value (0.0009 m DD^{-1}); and S_r=90% of the default value (270,000 m kg^{-1} DW). In addition, the root depth extension value was tested by setting values of q= 1.3 (default) and q=1.0.

Sensitivity analysis

A sensitivity analysis was carried out for three different parameters in the root model. These were the sensitivity of the root depth penetration rate (k_{rz}), which controls how fast the roots occupy a new soil layer and soil depth for roots distributed with the logarithmic function; the specific root length (S_r), used to calculate the root length in each soil unit influencing the potential and actual plant N uptake; and the root zone extension depth (q), which is the extra root zone where root density declines linearly below the simulated rooting depth. These three parameters were tested with a range of values for the form parameter in order to test their different influence on plant N uptake.

Comparison against experimental data

Values of soil mineral N depletion and root density distribution produced by the model were compared with the results from three field experiments, one including variable N supply for a white cabbage crop, one comparing N dynamics in short rotation sequences including vegetable crops with very different root growth (Thorup-Kristensen 2006b), and one comparing winter wheat and spring wheat with or without a preceding cover crop (Thorup-Kristensen et al. 2009)

In the first experiment white cabbage was transplanted on 18 April and harvested on 21 October 2004. Soil mineral N was measured on 12 May and 26 October 2004. For this study we selected five of the fertiliser levels (A–E) included in this experiment, represented by Y_1:Y_2, where Y_1 was the N application in the preceding year (2003) to a cauliflower crop, and Y_2 was the N application on 18 May 2004 (kg mineral N ha^{-1}). The treatments were: A: 0:0, B: 230:0, C: 0:120, D: 230:120 and E: 390:120. No N application in 2003 (Y_1=0) resulted in low mineral N content in spring, whereas the two higher levels of N application in 2003 left high residual N levels in the subsoil. Therefore this experiment is ideal for testing the ability to simulate deep root growth and N acquisition for this root model. The experiment is unpublished but information about soil and location has been reported elsewhere (Thorup-Kristensen 2006b). Simulated mineral N depletion of soil was tested with different a_z values of the white cabbage root model and compared with measured data from this experiment. Crop parameters adopted in simulations were DD_{lag} 100, k_{rz} 0.0014. In the simulation, the values 0, 1, 1.5, 2, 3, 4, 5, 6, 7, and 8 were tested for parameter a_z. Measured plant N uptake at harvest was compared with the a_z parameter. Measured soil mineral N values from the spring were used as initial conditions in the simulations and measured mineral N contents in late October in soil layers 0–1 m and 1–2 m were then compared with the values predicted by the model.

The validity of the model was also tested against data from an experiment with three different vegetable crops representing shallow-rooted (leek), deep-rooted with low root density (red beet) and deep-rooted with high root density (white cabbage). Leek, red beet and white cabbage were grown after a ryegrass cover crop or no cover crop in the preceding autumn, with two replicates, and the experiment was repeated in two years. Mineral N in the soil was measured on 18 May and 31 October 2001 and 16 May and 30 October 2002 (Thorup-Kristensen 2006b). Crop parameters adopted in the simulations were: DD_{lag} 200, k_{rz} 0.0004, a_z 8, a_x 8 for leek, DD_{lag} 250, k_{rz} 0.0009, a_z 2, a_x 2 for red beet, and DD_{lag} 100, k_{rz} 0.001, a_z 1.5, a_x 1.5 for white cabbage. Measured soil mineral N values from the spring were used as initial conditions in the simulations and measured mineral N contents in late October after vegetable harvest in the soil layers 0–1 and 1–2 m were compared with model simulated results.

Finally the model was tested against data from an experiment comparing winter wheat to spring wheat grown after a cover crop or with no preceding cover crop. The experiment was repeated in three years with different precipitation patterns. The crucifer cover crop was very deep rooted, and the spring and winter wheat crops reached rooting depths of c. 1 and 2 m depth respectively (Thorup-Kristensen et al. 2009). Measured soil mineral N values from August before sowing of winter wheat and the cover crop were used as initial conditions in the simulations and measured mineral N contents in four soil layers (0–0.5, 0.5–1, 1–1.5, and 1.5–2 m) in November and again after wheat harvest in August in the next year were compared to model simulated results. Crop parameters adopted in the simulations were: DD_{lag} 100, k_{rz} 0.001, a_z 2 for spring and winter wheat, and DD_{lag} 100, k_{rz} 0.0025, a_z 1.5 for the brassica cover crops.

Statistical analysis

Statistical analyses were conducted to evaluate the performance of the model in predicting soil mineral N using the Root Mean Square Error (RM+SE) approach. RMSE was calculated as shown in Eq. 7.

Here O_i was the observed value in the field experiment and P_i was the value predicted by the model, both with units (kg N ha^{-1}) and with n number of observations.

$$RMSE = \sqrt{\sum \frac{(O_i - P_i)^2}{n}} \tag{7}$$

Results

Root density distribution

Figure 1 shows the root length distributions obtained with different values of the parameter a_z after 110 days, equal to 1,400 DD and assuming a q=1.3 (Table 1). With form parameter a_z=0, the roots were distributed evenly in the soil profile to the current simulated rooting depth, while a_z>0 gave an exponential decline in root density with depth. When a_z> 3, the majority of the roots were found close to the soil surface. The fraction of root density in the extended zone (controlled by q) where root density decreases linearly with depth was high when a_z=0 compared with that calculated with higher a_z values.

Plant N uptake

In situations where the mineral N level in the topsoil was lower than the plant N demand, the form parameter had a significant impact on plant N uptake and soil mineral N depletion. Figure 2 shows model simulations with different form parameter values and their impacts on soil mineral N depletion, which has the same value as plant N uptake. The value a_z=0 resulted in fast plant N uptake and the highest N depletion from the soil. The form parameter value a_z=1 resulted in slightly slower uptake, whereas a_z=3 or 8 led to more significant reductions in N uptake.

Soil mineral N depletion occurred rapidly when roots reached the 0.25–0.5 m soil layer when a_z=0, 1 or 3, whereas a form parameter a_z=8 led to a rather slow depletion of this layer (Fig. 3a), when soil N contents were below plant N uptake demand. In the 1–1.25 m soil layer, a_z=0 and 1 led to a later but still rather fast mineral N depletion, but this depletion was slower for a_z=3 and a_z=8, where the fractions of plant N uptake compared to a_z=0 were only 0.52 and 0.01 respectively at the end of season. In this case, a test showed that when 40 kg N ha^{-1} were added as fertiliser on day 90 in the first soil layer, 99% of this was taken up within two days with a_z=8, while it took 12 days with a_z=0 (data not shown). Simulations where soil mineral N content exceeded crop N demand (Fig. 3b) showed similar differences, but against a background of generally much less efficient soil mineral N depletion. While high a_z values led to low subsoil root density, they increased topsoil root density and plant N uptake capacity.

Sensitivity analysis

The sensitivity of N uptake to variation in root depth penetration rate (K_{rz}) was moderate, as the reduction in N uptake was always less than 10% when depth penetration rate was reduced with 10% (Fig. 4a). With form parameter values a_z=1 and 3, plant N uptake interacted with root penetration rate,

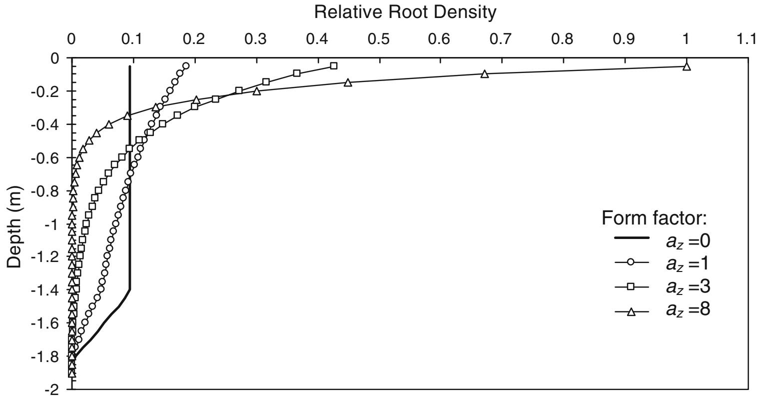

Fig. 1 Relative modelled root density distribution in soil profile after 110 days with different values of a_z. Total root biomass and root length were identical in all simulations. Default setting of root parameters include q=1.3

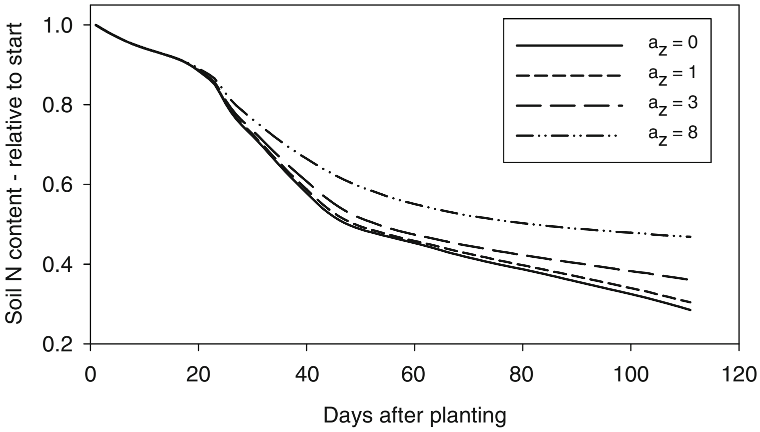

Fig. 2 Relative soil mineral N content in the 0–2.0 m soil layer compared with initial soil mineral N content for form parameter az=0, 1, 3 and 8 for default root model simulation in a situation where soil mineral N level was below potential plant N uptake

because with these a_z values the crop had the potential to produce high root densities and take N also in deep soil layers, and therefore a delayed depth penetration reduced uptake from deep soil layers. With a_z=8 plant N uptake was insensitive to root penetration rate (Fig. 4a), as even with the faster root penetration very few roots reached the deep soil layers. For all three a_z values the effect on N uptake relatively stronger during early growth, when the root system was still colonizing N rich upper soil layers.

Simulated N uptake was found to be sensitive to specific root length parameter (S_r) especially at very early growth stages, whereas during later growth stages the effect almost disappeared. During very early growth N uptake was reduced by 10% when S_r was reduced to 90% (Fig. 4b). The pattern of response did not vary depending on the a_z values.

Similarly to root penetration rate, the root zone extension factor q had a larger effect on the relative plant N uptake during the simulation with low form parameter values than with a_z=8 where only a small

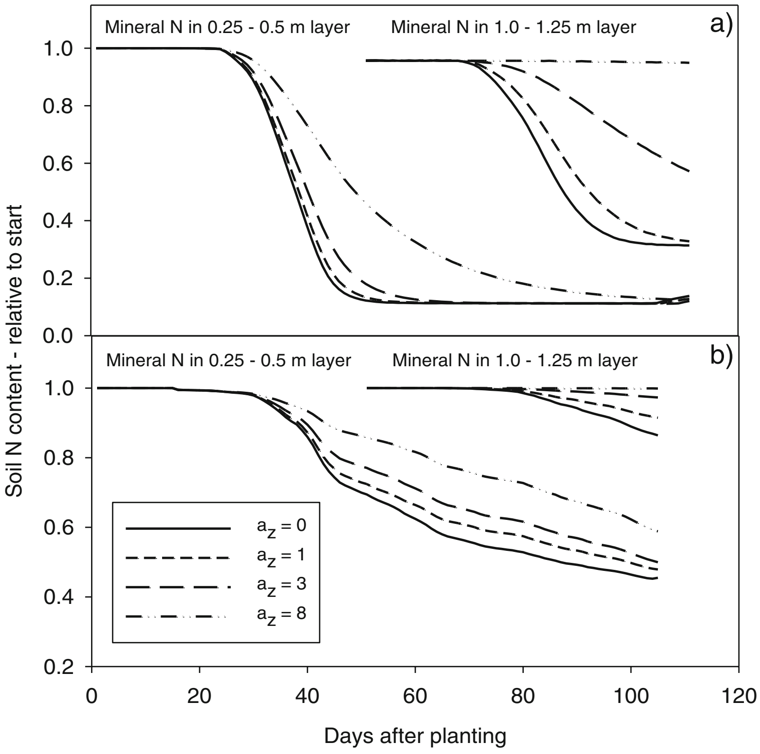

Fig. 3 Soil mineral N content in two soil layers, relative to initial start content for default root model for form parameter a_z=0, 1, 3 and 8 in 0.25–0.50 m and 1.00–1.25 m soil layers. a) Low N conditions, below potential uptake for the root model. b) High N conditions, exceeding simulated crop N demand

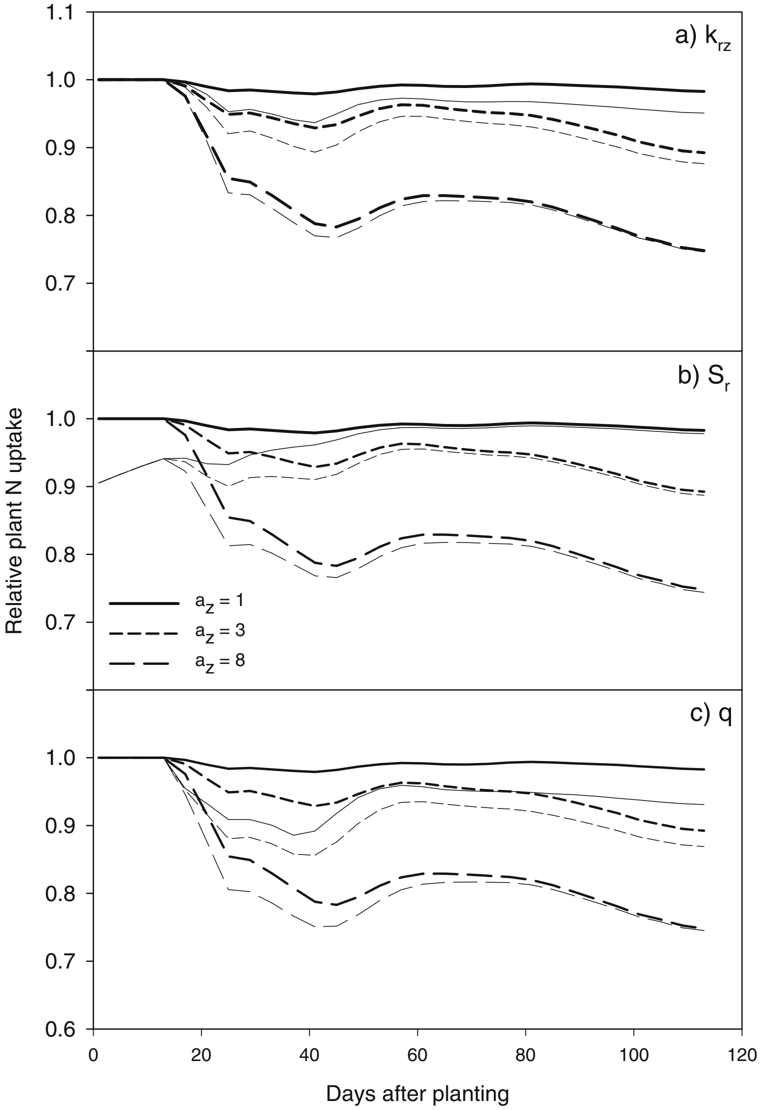

Fig. 4 Sensitivity of plant N uptake to three main parameters. Heavy lines show uptake using form parameter a_z=1, 3 and 8 relative to uptake with a_z=0. Thin lines show same simulations but with altered parameter values: a) root penetration rate (k_{rz}) reduced to 90% of default setting, b) specific root length (S_r) reduced to 90% of default setting, and c) without linear root part (q=1) compared to the default (q=1.3)

effect were seen and mainly seen during the period from 15 to 60 days after planting (Fig. 4c). Reducing *Krz* and removing the *q* factor both reduce root development at the deeper parts of the root system, and therefore mainly have an effect on root systems which have a significant part of their roots in the deeper part of the root system.

2-D simulation

Figure 5 shows simulated 2-D root density in a soil profile with three different a_x values for a crop grown with a row width of 1 m. Simulations with the form parameter values a_x=0 showed a high and evenly distributed root density in the surface layer. When a_x was increased to 3 or 8, the root density right below the crop row became higher and density in the soil between rows were reduced.

Figure 6 shows N depletion with three different row widths, simulated using a_z=3 and a_x=3. When row distance was only 0.1 m, and the model simulates the soil as a 1-D system, the crop depleted the soil mineral N by 50% in the 0.25–0.5 m layer within 40 days and had consumed all available soil mineral N by day 60. These values changed to days 50 and 75 for a row width of 0.5 m and to days 60 and 100 for a row width of 1 m (Fig. 6). With a row distance of 0.5 m and using the default model setup and

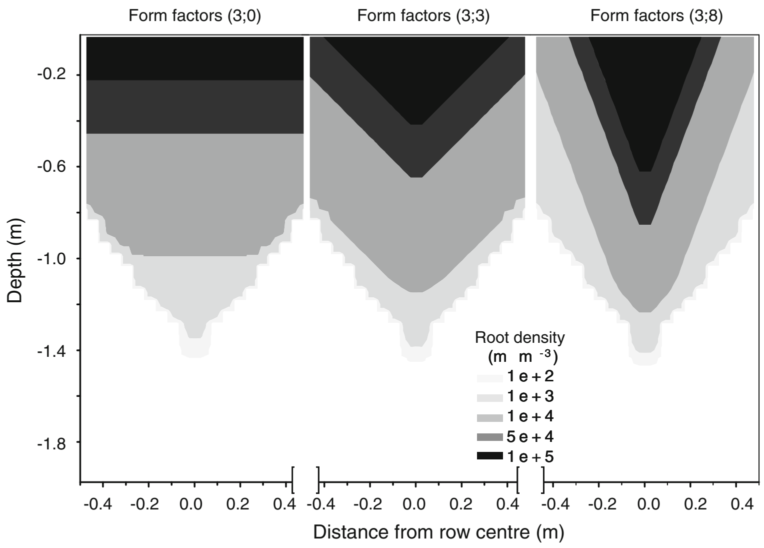

Fig. 5 Root density in the soil profile in a 2-D system. Three different form parameter settings were used in 2-D: (a_z;a_x), (3;0), (3;3), (3;8). Decreasing root density is indicated by decreasing intensity of shading

parameterization, the simulated N uptake showed very little sensitivity to variation in the a_z value (data not shown).

Model comparison against field experimental data

The value of the form parameter a_z for simulating root distribution was tested against data from field experiments. The distribution of roots into depth in the simulations matched root data for cabbage observed with minirhizotrons for days 46 and 64 reasonably well with a_z=1.5 (Fig. 7a, b), but not for day 153 (Fig. 7c). Simulated root distribution using a_z parameter values between 0 and 1.5 had a higher part of the roots below 1 m, and in this way they mimicked the field data from the last measurement date better, whereas when a_z>1.5 the match became very bad with far too low root densities below 1 m.

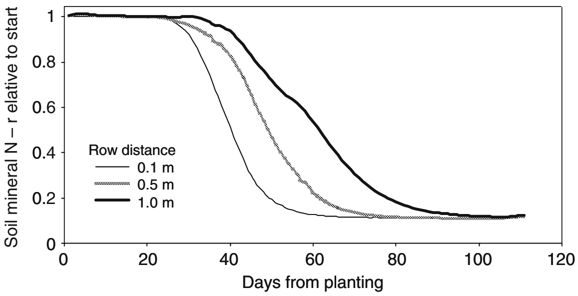

Fig. 6 Soil mineral N content relative to initial value for the default root model simulated in a system with low mineral N content. Relative soil mineral N content in 0.25–0.50 m soil layer with three different row widths, 0.1, 0.5, and 1.0 m. The 0.1 m row distance is simulated as 1-D. Form parameter values were a_z=3 and a_x=3

When the inorganic N content was lower than plant N uptake capacity and some soil mineral N was found in deeper soil layers, simulated crop N uptake was reduced at high a_z parameter values, and predicted plant N uptake was lower than experimental data, as illustrated with fertiliser levels A and B in Fig. 8a. When high N levels were found in the 0–1 m soil layer, plant N uptake in the simulations corresponded to field data and was not sensitive to the a_z value, as illustrated with fertiliser levels D and E. Mineral N left by the crop in different soil layers was highly affected by the different a_z values (Fig. 8b, c). For fertiliser levels A, B and C, the model depleted the 0–1 m soil layer to lower N levels than indicated by field data, and the sensitivity was less than at levels D and E, and at any fertiliser level in the 1–2 m soil layer. The model accurately predicted mineral N content in the 1–2 m soil layer for a_z=0 to 2, indicating that simulation of a high root density below 1 m depth is needed to simulate the N depletion measured in this soil layer in field experiments.

Comparing measured soil inorganic N data to simulations using different a_z values for three vegetable crops (Fig. 9) show that for cabbage the best fit (lowest RMSE) in both the 0–1 and 1–2 m soil layers were obtained with a_z=1.5. Especially in the subsoil the predictions became very bad with higher a_z values. With leek the RMSE values for the 0–1 m

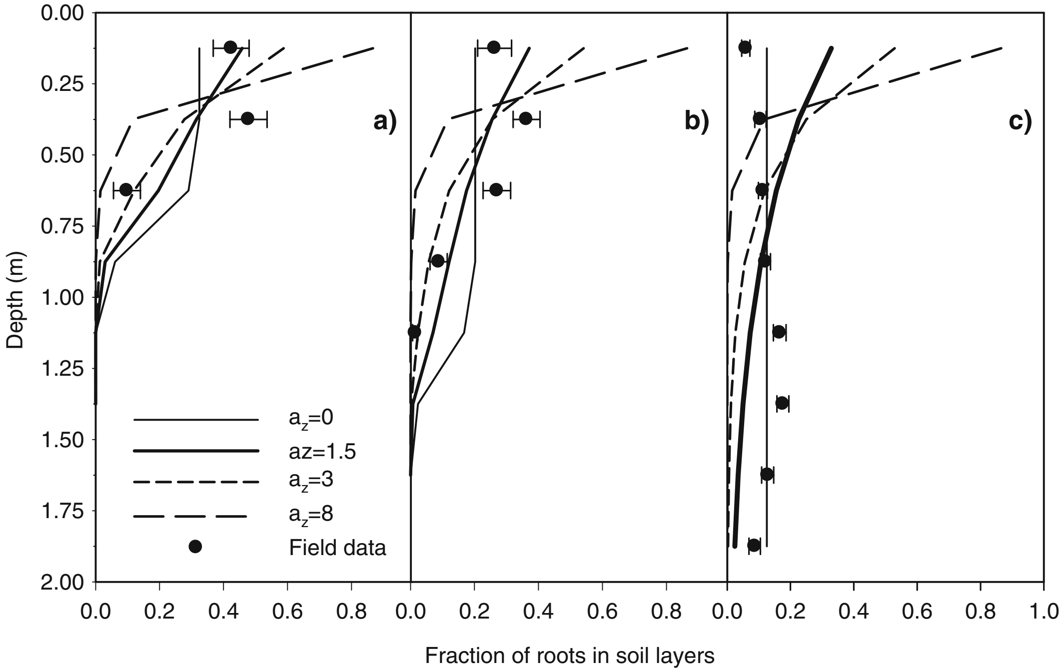

Fig. 7 Comparison of measured and simulated root density distribution of a white cabbage crop. The simulated data were obtained using a_z values ranging from 0 to 8. Field root data are the average from 10 different N fertility treatments obtained by variable N rates for white cabbage and a cauliflower pre-crop, and measured a) 46, b) 64, and c) 153 days after planting of white cabbage. *Values* are shown relative to the total root count at harvest, and *error bars* show SE (n=10)

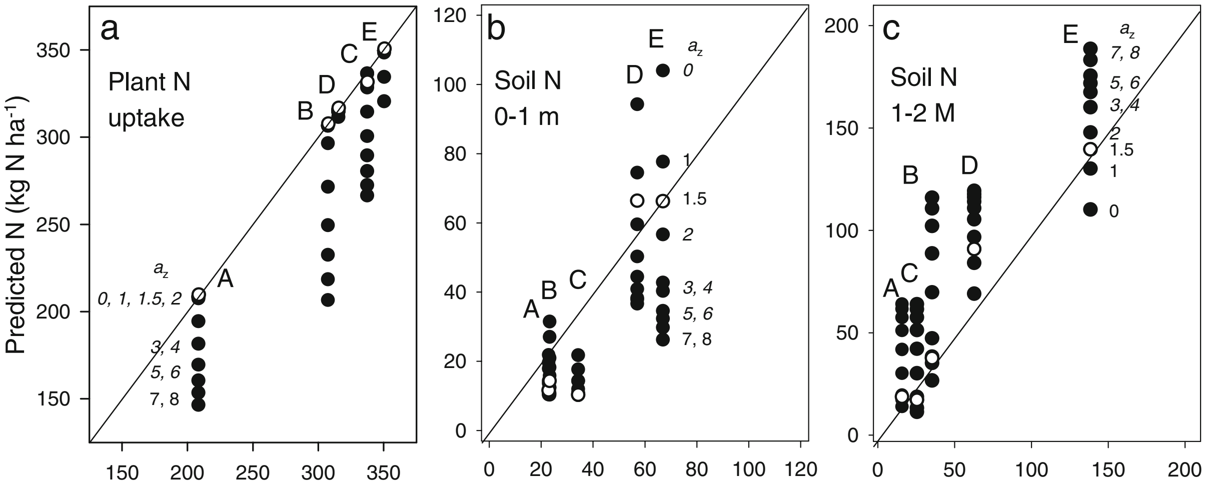

Fig. 8 Comparisons of measured and model simulated N results from white cabbage grown at five N fertilizer levels, and using different values of the form parameter a_z. a) Plant N uptake, b) soil mineral N in the 0–1.0 m soil layer, and c) soil mineral N in the 1.0–2.0 m soil layer. Data for each of the five fertiliser levels is shown (A to E, for fertiliser levels see Materials and Methods). All fertilizer levels were simulated using a_z=0 to 8 (Open symbols show a_z=1.5, filled symbols show a_z=0, 1, 2, 3, 4, 5, 6, 7 and 8

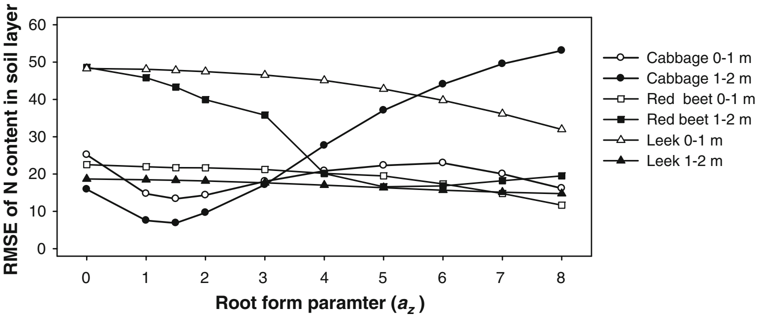

Fig. 9 RMSE of model predicted soil mineral N contents in the 0.0–1.0 and 1.0–2.0 m soil layers vs. measured results from experiments where variation in depth distribution of soil N had been created by pre-crops or cover crops grown in the previous year (see Figs. 8b and c, and Thorup-Kristensen, 2006b)

soil layer declined gradually with increasing a_z values, reaching its lowest value at $a_z=8$. In the 1–2 m layer there was no effect of changing a_z, in accordance with the fact that the simulated leek crop did not have any roots below 1 m (Fig. 10). With red beet a_z values between 4 and 8 showed low and almost constant RMSE values in both the 0–1 and 1–2 m soil layers, whereas high RMSE values in the 1–2 m soil layer were found using a_z values between 0 and 3.

When field observed root distribution of three vegetable crops was compared with simulations, the simulations of the leek root system matched observed data well (Fig. 10). Leek had a root distribution with high root density in the topsoil, and then declining fast with depth, corresponding to simulated root density distribution using high a_z values. Red beet also showed a reasonable match between measured and simulated data using $a_z=2$, though the model overestimated root density in the top 0.25 m, and underestimated root density somewhat between 1 and 1.75 m. Cabbage had a root distribution where the highest root densities were found between 0.75 and 1.5, a distribution which cannot be simulated by the root model, as also illustrated in Fig. 7c.

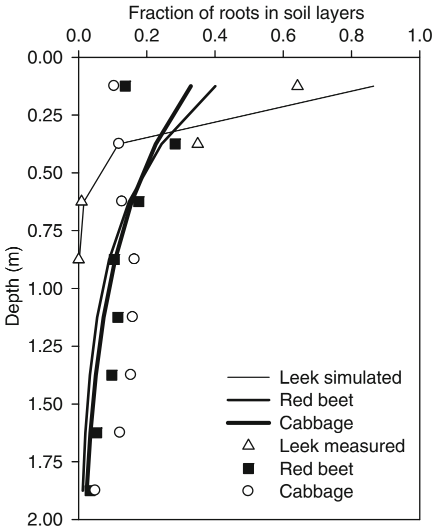

Fig. 10 Comparison of simulated (*lines*) and measured root intensity (*symbols*) for three vegetable crops. Root intensities in the field were measured on 5 September 2001 and 9 September 2002 as root intersections on grids in minirhizotrons. Field data are an average of 2 years and 2 replicates. All data are shown as fraction of total root density in all soil layers. Form parameter for leek was a_z=8, Red beet a_z=2 and white cabbage a_z=1.5

The simulated soil mineral N content after the three vegetable crops following either a ryegrass cover crop or no cover crop in the previous autumn was reasonably correlated with field observations in the 0–1 m and 1–2 m soil layers (Fig. 11). With no cover crop, the N content in surface soil layer was low and subsoil mineral N content was high. The model was able to simulate the effects of these different starting conditions, and their interaction with rooting depth of the three vegetable crops. Results revealed that leek only depleted the 0–0.5 m soil layer, due to its shallow root system, while red beet depleted the 0–1 m soil layer and white cabbage the whole 0–2 m layer for mineral N in the simulations, as well as in the field experiment. In the 0–1 m soil layer, the model underestimated soil mineral N content on the day of harvest by on average 33% or 10 kg N ha^{-1}. In the subsoil layer (1–2 m), the model underestimated soil mineral N content for red beet in the simulations without cover crops, whereas the results for leek and cabbage were in good agreement with the experimental data. Overall, the simulations therefore corre-

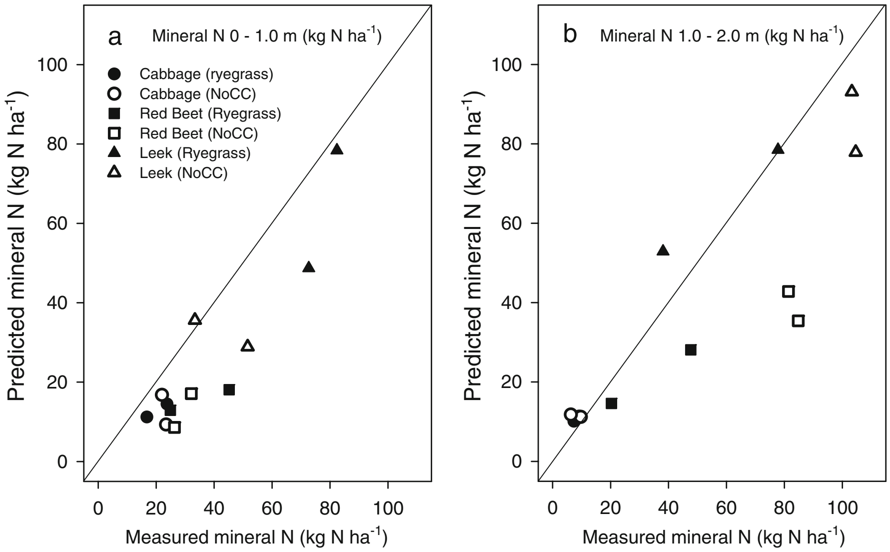

Fig. 11 Comparison of measured and predicted data on mineral N in the a) 0.0–1.0 m and b) 1.0–2.0 m soil layer. Simulations of three vegetable crops with ryegrass catch crop (*filled symbols*) or no catch crop (*open symbols*) in the preceding year. The experiment was repeated in two years, shown here with identical symbols. Key to symbols within diagram

sponded well with the large variation in soil mineral N content and depth distribution produced by the three very different root systems and the preceding cover crop effect.

Finally, the model was tested against a dataset including effects of crops with very different rooting depths and timing of root growth, leading to very different amounts and depth distributions of soil inorganic N. The crops were winter wheat, spring wheat, and a crucifer cover crop followed by spring wheat (Thorup-Kristensen et al. 2009). The simulation covered more than 12 months from sowing of the cover crop in early August to wheat harvest in August of the following year. The results show that the model is able to predict major effects of the experimental treatments and how they interact with weather conditions (Fig. 12). In all three years it simulates correctly the fact that the deep rooted crucifer cover crop is able to deplete soil inorganic N effectively to 2 in November. After wheat harvest in August it simulated repeatedly that spring wheat depleted the top 0.5 m as effectively as winter wheat, but that especially from 1 to 2 m much more inorganic N was left under spring wheat following bare soil than under winter wheat. In the 1–2 m soil layer it simulated that very little inorganic N would be present under winter wheat because of its deep rooting and under spring wheat grown after the cover crop, as the cover crop had prevented N leaching to this deep soil layer. The model was even able to simulate that soil inorganic N content under winter wheat was higher in the 1.5–2 m layer than in the 1–1.5 soil layer, as the winter wheat roots were not fully efficient in the deepest layer.

Discussion

Root penetration and density distribution

The assumption of an exponential decrease in root length density with depth has been adopted in several models, with a fixed low root density at the calculated rooting depth, but a varying form factor to distribute increased root length mainly with increasing root density in the uppermost soil layers (Abrahamsen and Hansen 2000; Barraclough and Leigh 1984; Greenwood et al. 1982). This exponential decrease has been shown to match monocots such as grasses and cereals reasonably well and was demonstrated here also for the vegetable crop leek, but not for dicot species such as oil radish or winter rape (Thorup-Kristensen 2001). In the model presented here, it is possible to vary the root length density distribution among soil layers, and to increase root length density in deeper soil layers using a fixed value of the form parameter but allowing root density to vary at calculated rooting depth. This variation in root distribution provides the opportunity to simulate a range of different crop species with significantly different root distribution. The model still had problems simulating the deep root distribution of dicot species such as white cabbage in late season (Fig. 7), but agreement was satisfactory in the earlier part of the

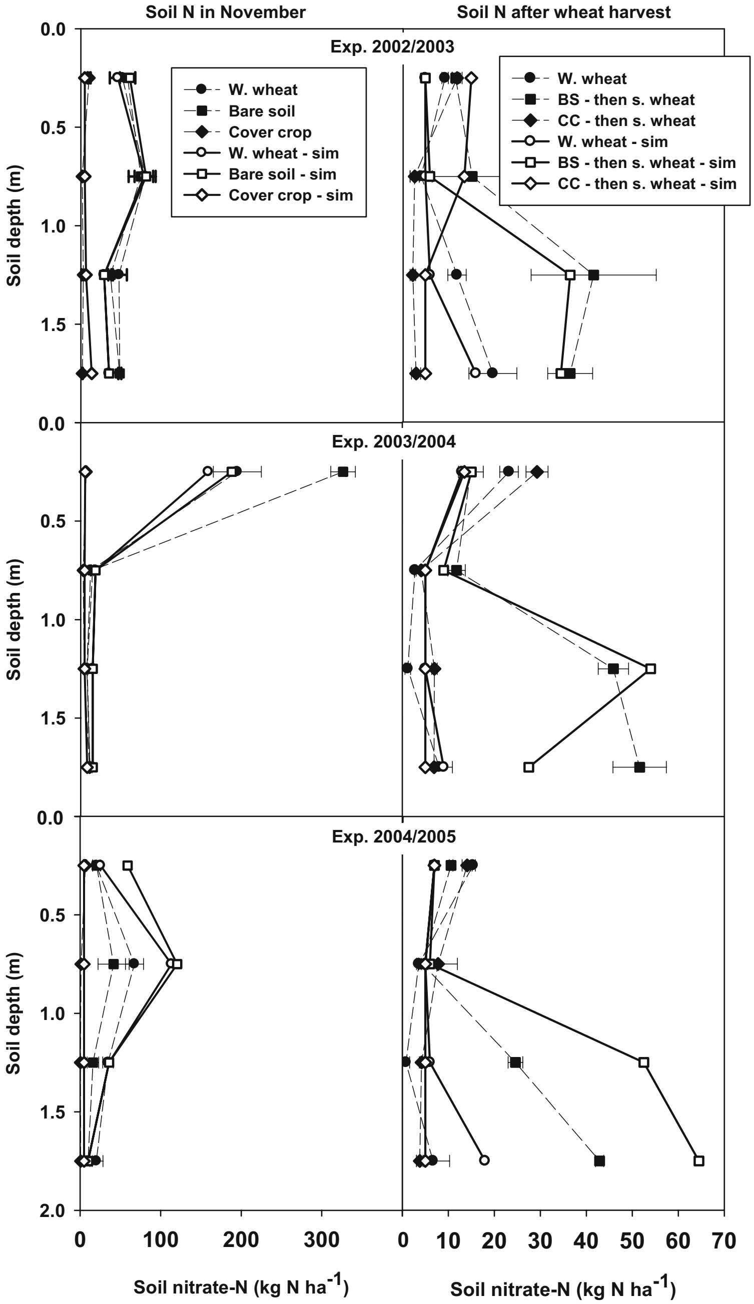

Fig. 12 Validation of model simulation of soil inorganic N content against 3 years of data from an experiment with winter wheat, spring wheat and cover crops (Thorup-Kristensen et al. 2009). *Left hand* plots show data from November under recently sown winter wheat, and in bare soil (BS) and cover crop (CC) plots where spring wheat are to be sown in the spring. *Right hand* plots show data from August in the next year after wheat harvest. *Closed symbols* show measured data, *open symbols* and *dashed lines* show model simulated data. *Error bars* show SE of measured data (n=3)

growing season. Using an exponential equation for root density distribution only fully agrees with most monocot species and some dicot species. However, the purpose of developing this model was not to simulate root depth distribution very closely, but mainly to develop a root model where it was possible to simulate crop N uptake from deeper soil layers more appropriately compared with existing crop models used today.

Plant N uptake

The root model showed plant N uptake from the entire rooted zone, even when there was a high N level in the topsoil. Field experiments with high mineral N level in the topsoil layer also show some plant N uptake from deeper soil layers, indicating that this approach complies with field observations

(Thorup-Kristensen and van den Boogaard 1998). Plant N uptake from all of the rooted zone was also supported by a field study where ^{15}N was added at 0.6 to 1.4 m depth in a carrot crop and from 1 to 2.5 m in a cabbage crop (Kristensen and Thorup-Kristensen 2004). For both crops a high N inflow rate was found from all positions within the estimated depth of the crop rooting zone, showing that the crops can deplete deep soil layers for mineral N. In a field experiment where sugar beet was grown, nitrate concentration was measured in three soil layers (0–0.2, 0.2–0.4 and 0.4–0.7 m depth) and these data showed a two-week delay in N depletion in the 0.4–0.7 m layer compared with the two layers above (Schmied et al. 2000). Furthermore, the two layers nearer the surface were depleted to the same soil mineral N concentration at harvest, whereas the deepest layer had a higher soil mineral N concentration. Such a delay in N depletion simulated by the model is also shown in Fig. 3, where depletion of the 1–1.25 m soil layer began at day 75. The efficiency of plant N uptake in this layer was dependent on the root density distribution, determined by a_z and plant N demand and mineral N level in soil layers above.

Simulated depletion of mineral N down the soil profile was highly sensitive to the value of the form parameter. This makes the description of the root distribution flexible and makes it possible to represent root systems from crops with very different root profiles. Sensitivity of plant N uptake to other parameters was also analysed. The root penetration rate was particularly important for simulation of crops with low a_z value, whereas in the simulations using a high a_z value the subsoil root density was low, and thus, absolute rooting depth became less important. For the same reason, simulation results are only sensitive to the q-parameter, when a_z is low. The sensitivity to the q-parameter may be too low at high a_z values, as Kristensen and Thorup-Kristensen (2004) found significant plant 15 N uptake from soil layers below the estimated rooting depth of carrot and sweet corn, crops which had a clear decline in root density with depth, i.e. a high a_z value.

During early crop growth the simulation of plant N uptake was sensitive to the specific root length (S_r), affecting total crop root length, but the importance of this parameter decreased during the simulation. In the beginning of the simulation a 10% reduction in the specific rooting length resulted in a 10% reduction in plant N uptake, but after about 50 days the effect had almost disappeared. Such a result is in accordance with the general observation that root growth can often limit crop nutrient uptake during early growth (e.g. Costigan (1988)), but later during growth the root system capacity for nutrient uptake is often much higher than the crop demand. Further, this pattern makes sense, as during early root colonisation of a soil volume, the roots will not yet have affected soil mineral N concentration, and the root length will be the main varying factor. Later, this will be compensated as high root density leads to fast soil mineral N depletion and therefore reduced uptake at a later stage, while soil volumes with fewer roots will sustain some plant N uptake for a longer time.

When fertilizer was added at the surface and in surplus of the plant N demand the simulations show that plant N uptake become independent of the a_z value, showing that the value of a_z is mainly important for crop N uptake when too little N is available in the topsoil. At high N supply the value of a_z only affects the depth distribution of N left in the soil. Further the test showed that the simulations with high a_z deplete the soil layer 0–1 m more effectively than is measured in the field. This opportunity to alter root distribution is important to allow plant models to describe mineral N dynamics in mixed rotations of arable and vegetable crops in low or reduced input agricultural systems, because root distributions differ strongly among arable and vegetable crops (Smit and Groenwold 2005; Thorup-Kristensen 2006b) and with a demand for reduced N fertilization to protect the environment, less fertilizer N will be added and there will be more focus on cover crop use and utilization of residual mineral N in deeper soil layers.

Comparisons between measured and simulated vegetable crops of leek, red beet and white cabbage (Figs. 8 and 11) showed that the model could be parameterized to simulate the measured depletion of N from the 0–1 m and 1–2 m layers in the autumn at vegetable harvest. This was found on a background of very different N content in the 1–2 m soil layer in the spring before planting of vegetables. This was possible even though the simulated root distribution does not comply accurately with the root distribution measured in the field (Fig. 10), but it has previously been shown that rooting depth may be more important than root density distribution for determining the ability of crops to deplete soil inorganic N (Thorup-

Kristensen 2001). Robinson et al. (1994) showed another example based on a ^{15}N study, where soil mineral N was depleted most efficiently by the crop with the lowest root length density, in this case because of interactions with above ground plant N status.

The strongest deviation between measured and simulated data was found for red beet in the 1–2 m soil layer (Fig. 11), where the model simulated lower N content than found in the experiment. This is also the reason why the model optimization showed that an a_z value above 4 would give the best simulation of red beet soil N depletion (Fig. 9), while it would clearly not simulate a root system matching the one measured on red beet. This deviation may be due to the simplicity of the crop model used. In this model crop growth, root growth and N uptake continues at full rate until the date of harvest. This is relevant for many of the vegetable crops the EU_Rotate model was developed to simulate, but not for all. Root and tuber crops as onion, potato, red beet, and carrot will cease to produce leaves during late growth stages while tubers are still growing. Thus, the observation that red beet did not effectively deplete the deeper parts of its root zone may be due to a low N demand at the late part of its growth period, when the deeper parts of the root system were developed. In the model simulation this result can be mimicked by using an unrealistically high value of a_z, to create a very low subsoil root density. However, developing a crop growth model allowing reduced N demand at late growth stages would be more relevant, also for simulation of cereal crops which mature and die off at the end of their growth.

Row crops such as carrots and maize have different rooting depth and root density beneath the crop rows and in the interrow soil. This root distribution leads to a lower or delayed N depletion in the soil between rows, as has been demonstrated in field experiments (Liedgens and Richner 2001; Schröder et al. 1996; Thorup-Kristensen and Van den Boogaard 1998). The model showed high sensitivity to row distance, but did not show high difference in N depletion with variation of the a_x form parameter. The model simulations are likely to be more sensitive to variation in a_x when simulating crops with slow root growth, than with the faster root growth in the tests made here, but there is a lack of experimental data available to qualify such tests. The 2-D model will be useful for simulating the delay in soil mineral N availability to row crops compared to other crops, which will be especially important for vegetable crops which are harvested at early growth stages.

All in all we find that the root model presented in this paper is an improvement compared to other simple root models used for crop-soil N simulation models. It can simulate the variable ability of crop species to build high root density and N uptake capacity in deep soil layers, and do so in a very simple way. The tests of the ability of the root model as part of the full EU-Rotate model to simulate effects of cover crops and main crops with highly variable root growth and timing of root growth shown in Figs. 11 and 12 demonstrate that it allow the model to simulate main effects of roots on N use efficiency which is important e.g. for model simulations of environmental effects.

Conclusions

The root modelling approach used in the present study involved simulating the development of rooting depth, root density distribution with depth, and plant N uptake. The model can be parameterised to simulate observed differences in root growth among species of vegetable and arable crops using only a few parameters, such as root system form, lag phase for germination and root penetration rate. This model could simulate experimental data for root distribution of monocot crops, whereas for deep-rooted dicot crops, the simulated root density in the lower part of the rooting zone were too low compared with experimental data. However, by varying the a_z value, the model was capable to predict N depletion in surface and subsoil layers reasonably well after crops with different N demand, rooting depth and depth distribution of the root system, which is important for simulating nitrogen use efficiency as well as nitrogen losses from agricultural and horticultural rotations. The 2-D root model approach used made the model able to simulate soil mineral N depletion both horizontal and vertically to comply with different row width and rooting depths.

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