Aspects of nitrogen use efficiency of cauliflower I. A simulation modelling based analysis of nitrogen availability under field conditions

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SUMMARY

Data from several field experiments (eight crops grown under a widely varying nitrogen supply on a loess loam soil) were used for a simulation modelling based analysis of nitrogen availability of cauliflower. The model was built out of components describing root growth, nitrate transport to the roots and the vertical nitrate transport within the soil.

Root observations obtained over 2 years indicated an increased fraction of dry matter allocated to the fine roots under N deficiency. An adapted version of a root growth model for cauliflower described the rooting data with an $R^2 = 0.75$. Based upon an acceptable description of the soil water budget, vertical nitrate movement during the growth period of cauliflower was accurately described. The magnitude of this movement, however, was limited to soil depths of about 60 cm even after periods of high rainfall, because of a high soil water holding capacity. An analysis of the factors determining nitrate availability indicated that apparent mass flow was only of high importance for conditions of extremely high N supply where high amounts of nitrate nitrogen remain in the soil up to the end of the growing season. Otherwise, the dominating fraction of nitrate has to be transported to the roots by diffusion. Single root model based calculations of maximum nitrate transport to roots overestimated N availability as indicated by estimates of critical soil nitrate N that were too low. The introduction of a restricted uptake activity period of the roots was used to bridge the gap between theoretical calculations and empirical results. Scenario calculations were carried out to obtain functional relationships between N supply and residual soil nitrate levels for different soil conditions and management practices.

INTRODUCTION

Crops from intensive vegetable cropping systems like cauliflower often have high nitrogen uptake rates because of high nitrogen contents of their organs and high growth rates (Van den Boogaard & Thorup-Kristensen 1997; Schenk 1998). However, these crops also have mostly comparable low total root lengths (Jackson 1995), especially when cultivated as transplants (Thorup-Kristensen 1993; Kage *et al.* 2000). This agronomic practice shortens their growth period on the field and thereby the time available for the root system to exploit the soil volume. High specific nutrient influx rates therefore have to be maintained throughout the crop's growing period in order to ensure maximum growth (Burns 1980). Under similar conditions this is only possible with higher soil nitrogen contents than for crops with higher total root length. Higher residual soil nitrogen contents, however, may lead to leaching losses and therefore to a decrease of the nitrogen use efficiency of the cropping system and to environmental pollution (De Neve & Hofman 1998).

Because of the high mobility of the nitrate ion in the soil solution most crops are able to exhaust the soil down to very low nitrate concentrations and thereby sustain nitrate influx rates sufficient for satisfying the nitrogen demand of the crop (De Willigen &

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Table 1. *Type of experiment (LT = long term, A = annual), year, planting and harvest dates, average incident photosynthetic active radiation, I, and average temperature during the growth period of the cauliflower experiments used in this study*

Type	Year	Planting date	Harvest date	Average I (MJ/m² per day)	Average temperature (°C)	No. of N treatments
LT	1994	97	185	8·13	13·12	2
LT	1994	207	293	5·45	14·52	2
LT	1995	94	187	7·59	12·13	2
LT	1995	200	291	6·10	16·49	2
LT	1996	100	189	7·41	12·59	2
LT	1996	200	284	6·18	14·34	2
A	1996	170	240	7·78	16·08	4
A	1997	190	258	7·23	18·56	4

Van Noordwijk 1987*a*). Critical conditions for nitrate availability can therefore be found in the sub soil, where rooting density is low (Wiesler & Horst 1994) or for crops with very sparse root systems (Kage 1997).

Kage *et al.* (2002) showed that for a loess loam soil under ample water supply amounts of soil mineral nitrogen of about 40–50 kg N/ha in the upper 60 cm of the soil profile must be maintained to sustain leaf protein contents of cauliflower at an optimal level. Such an empirical analysis is hampered by the fact that changing soil conditions, an altered water regime or a different distribution of the mineral nitrogen in the soil profile may change considerably this empirical value for critical soil mineral nitrogen contents.

The aim of the present paper therefore is to analyse the availability of soil nitrogen for cauliflower using a mechanistic model approach. For this purpose a previously published model for root growth of cauliflower (Kage *et al.* 2000) is combined with a mechanistic model for soil nitrate availability (Baldwin *et al.* 1973; Kage 1997) based on the single root approach (Gardner 1960). Data from two annual and one long-term field experiments summing up to eight crops grown over a wide range of nitrogen supply are used for the analysis in the present paper. Furthermore scenario calculations were carried out to quantify potential leaching losses during the growing period on a hypothetical sandy soil and to derive functional dependencies between nitrogen supply rate and residual soil nitrate levels.

MATERIAL AND METHODS

Field experiments

The field experiments used in the present study belong to two different groups. The first group is from two annual nitrogen fertilization trials from 1996 and 1997 (Alt 1999). Additionally, data from a long-term crop rotation experiment are used for further model evaluation. These experiments have previously been described in Kage & Stützel (1999*b*), but for the present study reduced N supply treatments are also included in the analysis.

All field experiments were conducted on the same experimental farm located 15 km south of Hannover, Germany, on a typical loess derived hapludalf soil. Crops were established in the field using transplants grown in peat cubes of 4 cm edge length and the average visible leaf number at planting ranged from 2·9 to 4·03 leaves per plant. Crop husbandry in all experiments was designed to ensure that crop growth was not limited by the availability of water. Pesticides were applied when needed to ensure healthy growth.

Nitrogen fertilization was given as ammonium nitrate at the time of transplanting only for the annual experiments. Soil nitrate content of 10–15 kg N/ha in 1996 and 1997 in the 0–60 cm soil layer were subtracted from 150 (N1), 300 (N2) and 450 kg/ha (N3) target values. Furthermore a N0 treatment was included, which received no nitrate nitrogen. For the long-term experiment a nitrogen fertilization schedule according to the KNS system (Lorenz *et al.* 1989) was applied, defining two target values of 130 kg N/ha from 0–30 cm soil depth at transplanting and of 270 kg N/ha from 0–60 cm soil depth about 4 weeks after transplanting. The two N treatments received either 100% of this recommended N supply level or a reduced N supply of 70% of this level in 1994 and 1995 and of 50% of this level in 1996.

Temperature and radiation data were taken from measurements of an automated weather station (Campbell Sci. Ltd., UK) located on the experimental station. Measured values of global radiation were converted to photosynthetic active radiation, I, using a factor of 0·5 (Szeicz 1974). Average values of I and air temperature at 2 m height for the experimental years are shown in Table 1.

Soil cores were extracted at the last harvest of the annual experiments in 1996 in all nitrogen treatments and in 1997 in the N0 and N2 treatment only using a special root auger of 8 cm diameter (Eijkelkamp

Agriresearch Equipment, Giesbeek, NL) down to a depth of 90 cm in 15 cm increments. Samples were taken at two positions within a field plot, one beneath a cauliflower plant and one in a mid-row position. Soil cores were stored at 4 °C until roots were washed out over a 1·25 mm sieve and root length was determined after removing organic debris from the sample using the method of Newman (1966).

Soil mineral N was determined down to a depth of 120 cm in four intervals of 30 cm thickness. From every plot six auger samples were collected. Soil nitrate N was measured photometrically at a wave length of 210 nm after extraction with 0·025 N CaCl$_2$ (Navone 1964). One tensiometer per plot was installed shortly after transplanting at depths of 20, 40, 70 and 90 cm, respectively in the annual experiment in 1997 and in the crops of the long-term experiment.

There was generally an exceptionally high variation in the data of soil water tension and soil nitrate for the late planted crops of the long-term experiment (Table 1). The reasons are the need for irrigation of these crops, which was carried out using a micro sprinkler technique inducing a substantial local variation of water supply, and the incorporation of crop residues from the previous cauliflower crop. From these crops only net mineralization data are presented here.

Calculation of net mineralization

Net mineralization was calculated for every treatment and for periods between soil and plant analyses separately from the data of soil nitrate nitrogen from 0–120 cm and measurements of shoot dry matter and nitrogen content. An additional amount of 10 and 5 % of measured shoot nitrogen was assumed to be located in the root part of the fertilized and unfertilized plants, respectively, and net mineralization was corrected for that.

Model

Root growth

The root growth model module used in this study is described in detail by Kage *et al.* (2000). Roughly, it calculates the total root length based on the fraction of dry matter allocated to the root system and using a constant average specific root length for conversion of root dry matter into root length. The increase of rooting depth is derived using a simple temperature sum based approach and the vertical distribution of root length is described using a negative exponential function. However, some modifications of the original model module are included to account for (a) the effects of root ageing on water and nitrogen uptake and (b) the effects of an altered dry matter partitioning under nitrogen stress.

The nitrate uptake properties of roots clearly change during ageing, therefore a decrease of the maximum nitrate capacity can be observed (Reidenbach & Horst 1997). The assumption that all roots are fully active in nitrate and water uptake, which is often made within crop growth models (Benjamin *et al.* 1996), is therefore invalid. However, studies on the temporal change of root activity under field conditions are still lacking. We therefore tried to bridge this knowledge gap in a very simple way. Roots are assumed to be fully active during a certain time span from their initial occurrence (active duration, *AD*) and are assumed to be fully non-active afterwards. Using this simplification it is possible to calculate an effective root length RL_{eff} and rooting density RLD_{eff} for all soil layers, *i*, from the total root length and their distribution in different age classes, *j*:

$$RL_{eff_i} = \sum_{j=1}^{j \times dt \leqslant AD} RLmat_{i,j} \qquad (1)$$

The two dimensional matrix RL_{mat} is updated in daily time steps, thereby all elements of the matrix are shifted one step forward in the time dimension, *j*:

$$RL_{i,j} = RL_{i,j-1} \qquad (2)$$

The first grid cell in every layer becomes the actual increase in root length, if positive:

$$RL_{i,1} = \max\left(0, \frac{dRL}{dt}\right) \qquad (3)$$

From the effective root length, the effective root length density is calculated:

$$RLD_{eff_i} = RL_{eff_i}/\Delta z \qquad (4)$$

It is well known that the fraction of assimilates allocated to the roots increases under restricted nitrogen (Ericsson 1995) or water supply (Huck *et al.* 1986) and this behaviour motivated the postulation of the functional equilibrium law (Brouwer 1962). In the present work, this effect is also considered in a simplistic manner, assuming that the fraction of assimilates allocated to the fine roots, f_{fr} (−), is increased to a maximum value f_{frmax} during periods of nitrogen deficiency, i.e. when the N demand, N_{dem} is higher than the N supply, N_{sup}, and decreased to the value of unstressed plants f_{fr0} if the nitrogen supply is sufficient:

$$\frac{df_{fr}}{dt} =$$
$$\begin{cases} f_{fr} \times r_{ffr}\left(1 - \dfrac{f_{fr}}{f_{frmax}}\right) & N_{dem} > N_{sup} \\ -(f_{frmax} - f_{fr} + f_{fr0}) \times r_{ffr}\left(1 - \dfrac{f_{fr}}{f_{fr0}}\right) & N_{dem} \leqslant N_{sup} \end{cases},$$
$$(5)$$

Thereby the parameter r_{ffr} (per day) determines the rapidity of the adaptation process. Here an estimated

Table 2. *Parameters of the Van Genuchten–Mualem equations found by fitting to data on soil water tension* v. *soil water content*

Soil	Depth (cm)	θ_r (cm³/cm³)	θ_s (cm³/cm³)	α per cm	n	l*	K_s* (cm/day)
Loess loam	0–30	0·0	0·4295	0·01479	1·276	0·5	7
	30–80	0·0347	0·4367	0·00903	1·448	0·5	7
	80–200	0·0	0·4485	0·00675	1·238	0·5	7
Sandy (Scenario)	0–30	0·0	0·4429	0·0332	1·336	0·5	40·19
	30–200	0·0	0·3800	0·01997	1·627	0·5	50

* Estimated value.

value of 0·2 was used, assuming that the shift of the allocation process has a time scale in the order of days rather than hours or weeks.

Water transport

Vertical water transport in the soil profile is calculated using the water content-based formulation of the Richard's equation. The relationships between soil water diffusivity and the volumetric soil water content were described using the functions suggested by van Genuchten (1980) in the revised form of Wösten & Genuchten (1988). The necessary parameters for this relationship were estimated with the program RETC (van Genuchten *et al.* 1991) using data from Künkele (1996) and H. Bohne (1999, personal communication) for the loess loam soil of the experimental site. Additionally, parameters for a sandy soil were derived for a scenario calculation using data taken from Wösten *et al.* (1986) (Table 2).

The sink term $S(\psi)_{,i}$ in the layer i of the finite difference scheme is calculated from a hypothetical maximum sink term $S_{max}(\psi)_{,i}$ that is defined by the following equation:

$$S_{max,i}(\psi) = T_p \frac{RLD_i^{cf}}{\sum_1^{n_r} RLD_i^{cf}} \qquad (6)$$

where T_p is the potential transpiration rate, RLD_i is the rooting density in the layer i, n_r is the number of the rooted compartments computed from the maximum rooting depth z_r and the thickness of the layers, Δz. The parameter cf is an empirical factor that accounts for root competition. This factor is set to a value of 0·5 according to the results of Ehlers *et al.* (1991) and Kage & Ehlers (1996).

The maximum sink term $S_{max}(\psi)_{,i}$ is converted to the actual sink term $S(\psi)_{,i}$ by multiplication with an empirical reduction factor $\alpha(\psi)$ as described by Feddes *et al.* (1978). This factor was assumed to decline from a value of one at matrix potentials $\geqslant -1000$ hPa down to zero at $-20\,000$ hPa.

Evapo-transpiration

Potential evaporation is calculated using the Penman–Monteith equation (Monteith 1973). Net radiation,

R_n, was computed from the global radiation, GR, using an empirical regression equation derived from measurements of global and net radiation over grass at the experimental field 'Ruthe':

$$R_n = 0.6494 \times GR - 18.417 \qquad (7)$$

Potential evaporation is the sum of potential transpiration, T_p, potential evaporation, E_p, and of interception evaporation, I:

$$ET_p = T_p + E_p + I \qquad (8)$$

Interception evaporation kg/m² per day is assumed to take place from a storage pool, IP (kg/m²), situated on the surface of the canopy. The capacity of this storage pool, CIP (kg/m²), is calculated from a specific interception capacity, SIC (kg/m² per m²), and the leaf area index LAI m²/m².

$$CIP = SIC \times LAI \qquad (9)$$

Interception is the minimum of the sum of the maximum possible change of the interception pool and the precipitation rate, Pr, kg/m² per day and the potential evapo-transpiration:

$$I = \min(IP/\mathrm{d}t + \min(\mathrm{Pr}, CIP - IP), ET_p) \qquad (10)$$

The change of the storage pool is calculated from the minimum of the precipitation rate and the actual unused capacity of the precipitation pool, $CIP - IP$:

$$\frac{\mathrm{d}IP}{\mathrm{d}t} = \min(\mathrm{Pr}, CIP - IP) - I \qquad (11)$$

The potential evaporation rate is determined by the fraction of radiation energy which is reaching the soil surface. This value is computed from the leaf area index of the crop and the extinction coefficient for global radiation.

Actual evaporation was determined from an empirical function using potential evaporation and the water potential in 10 cm depth as input parameters (Beese *et al.* 1978). The potential transpiration is calculated as the remaining part of the potential evapo-transpiration after subtracting potential evaporation and interception and also taking into account an empirical crop resistance.

Soil nitrogen balance

In well-aerated soils the concentration of ammonium is usually very low compared with that of nitrate, therefore only nitrate nitrogen is considered by the model.

Vertical nitrate transport

Vertical nitrate transport in the soil profile is calculated by a numerical solution of the convection-dispersion equation (Addiscott & Wagenet 1985). The initial condition for this equation was the measured nitrate concentration from 0 to 120 cm, which was determined in a spatial resolution of 30 cm. Since no N_{min} measurements were available for depths below 120 cm, all layers from 100 to 200 cm were initialized with the measured N_{min} content of the layer 90–120 cm depth.

Nitrate uptake by plant roots

It is assumed that the nitrate uptake by the plants root system UR_{act} (g N/m² per day) is determined either by the nitrogen demand of the plants N_{dem} or the maximum nitrate transport rate to the root system UR_{max}:

$$UR_{max} < N_{dem}: \quad UR_{act} = UR_{max}$$
$$UR_{max} > N_{dem}: \quad UR_{act} = N_{dem} \tag{12}$$

Nitrogen demand of plants is derived from the sum of demand of the plant organs:

$$N_{dem} = \sum N_{dem,i} \tag{13}$$

The latter is computed from their growth rate and their nitrogen content under optimal N supply as described in Kage *et al.* (2000).

Nitrogen transport to roots

The maximum nitrogen transport rate to roots, I_{nmax} (g N/cm per day), is calculated using the single root model approach (Gardner 1960) for which Baldwin *et al.* (1973) developed an analytical solution assuming steady state conditions. A modified version of this equation was used in the present study. For details of the derivation of this equation see Kage (1997).

In this equation a minimum concentration C_{lmin} is used, defined as the lowest concentration where nitrate uptake matches transport to roots (De Willigen & Van Noordwijk 1987a). Since most plant species (Peuke & Kaiser 1996) are very efficient in nitrate uptake, this value will be usually very low ($<10^{-7}$ mol/cm³), which is equivalent to less than 1 kg N in a 30 cm soil layer, a volumetric water content of 30%. Therefore, the exact value of this parameter is not very important and can be set to zero, as it was done in the present study, in order to calculate the maximum uptake rate.

For each rooted soil layer i the maximum nitrate uptake rate $AR_{max,i}$ (g/cm per day) is computed from the maximum nitrate influx rate $I_{nmax,i}$ (g/cm per day) and the root length in that particular layer RL_i (cm/cm²):

$$AR_{max,i} = I_{nmax,i} \times RL_i \tag{14}$$

The maximum N supply rate (N_{sup}) (g N/m² per day) is then simply the sum of all maximum uptake rates corrected for the changed units of area:

$$N_{sup} = \sum AR_{max,i} \times 10^4 \tag{15}$$

The sink term of the convection dispersion equation then is computed either from the nitrogen demand and the proportion of the maximum nitrate uptake rate to the sum of the maximum uptake rate in all rooted soil layers, or if the sum of the maximum uptake rates is smaller than the nitrogen demand the sink term is simply the maximum uptake rate itself:

$$S_i = \begin{cases} AR_{max,i} & N_{dem} \geqslant N_{sup} \\ N_{dem} \times 10^{-4} \times \dfrac{AR_{max,i}}{\sum_{i=1}^{i\Delta z = z_r} AR_{max,i}} & N_{dem} < N_{sup} \end{cases} \tag{16}$$

The total N uptake rate, UR_{act}, from the soil then is the sum of the sink terms in all soil layers.

Parameter estimation and statistics

The whole model is implemented within the HUME modelling environment (Kage & Stützel 1999a). This modelling environment supports parameter estimation based on the Marquardt algorithm (Marquardt 1963). The parameter estimate for f_{fRmax} (Eqn 5) was obtained by minimizing the squared sum of differences between measured and simulated RLD values from the annual experiment in 1996.

For evaluation the goodness of fit of the model output linear regression analysis and the statistical measures modelling efficiency (EF) and root mean square error ($RMSE$) used:

$$EF = 1 - \frac{\sum (y_i - \hat{y}_i)^2}{\sum (y_i - \bar{y}_i)^2} \tag{17}$$

$$RMSE = \sqrt{\frac{\sum (y_i - \hat{y}_i)^2}{n}} \tag{18}$$

where y_i and $\hat{y}_i$ are the measured and predicted values, respectively and n is the number of observations.

RESULTS

There is a tendency of decreasing net mineralization rates with increasing nitrogen fertilization (Table 3) in the annual experiments. For the rotation experiment no clear influence of nitrogen fertilization on calculated net mineralization could be found. For the

Table 3. *Calculated average net mineralization rate (kg N/ha per day) during crop growing period in two experimental years under four different nitrogen supply rates (N0–N3)*

N supply rate	1996	1997
N0	0·728	1·173
N1	0·014	0·835
N2	−0·168	0·709
N3	1·276	0·386

Table 4. *Calculated average net mineralization rate (kg N/ha per day) in three experimental years under two different nitrogen supply rates* (N_{norm}, N_{red})

	1994		1995		1996	
Planting	Early	Late	Early	Late	Early	Late
N_{norm}	0·517	5·389	0·241	0·847	0·509	1·75
N_{red}	0·242	3·414	0·650	1·059	0·510	0·92
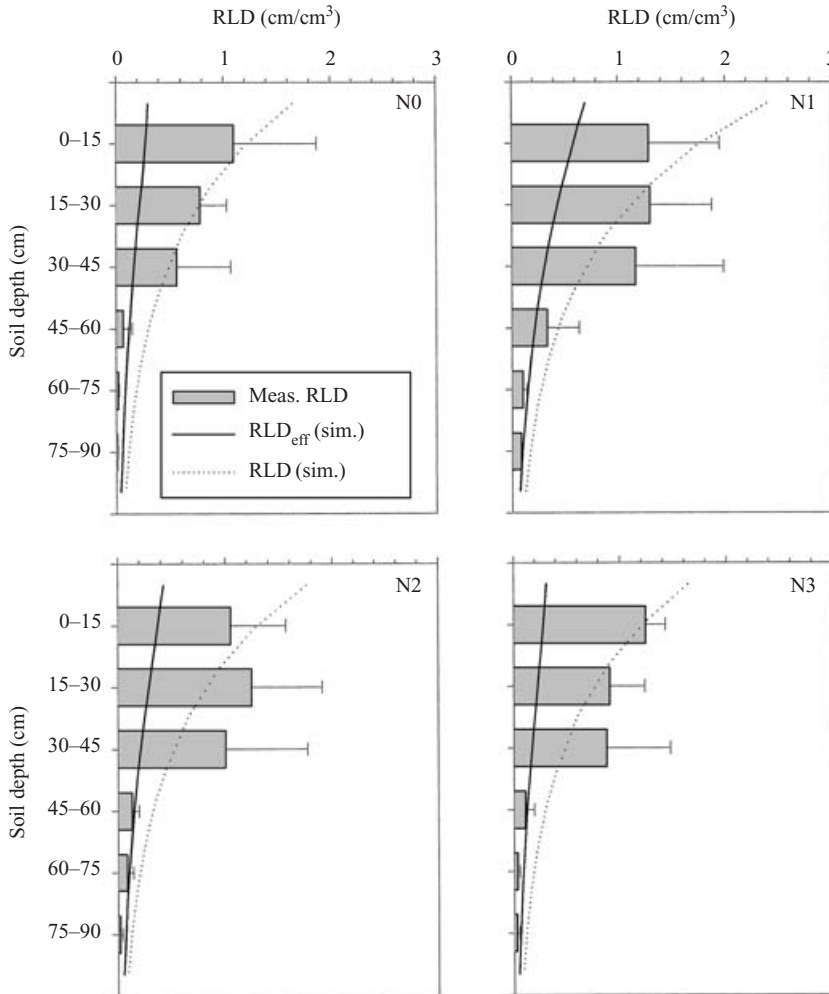
Fig. 1. Measured and simulated root length density (*RLD*) *v.* soil depth at end of the growing period for cauliflower crops grown under 4 different N supply treatments (N0 … N3) in 1996. Simulated *RLD* is shown for total (*RLD*) and effective root length density (*RLD*$_{eff}$). Error bars indicate standard error of the mean. The linear regression equation between measured and simulated *RLD* is $y = 0.17(\pm 0.0884) + 0.95(\pm 0.12)x$, $R^2 = 0.75$, $n = 24$.
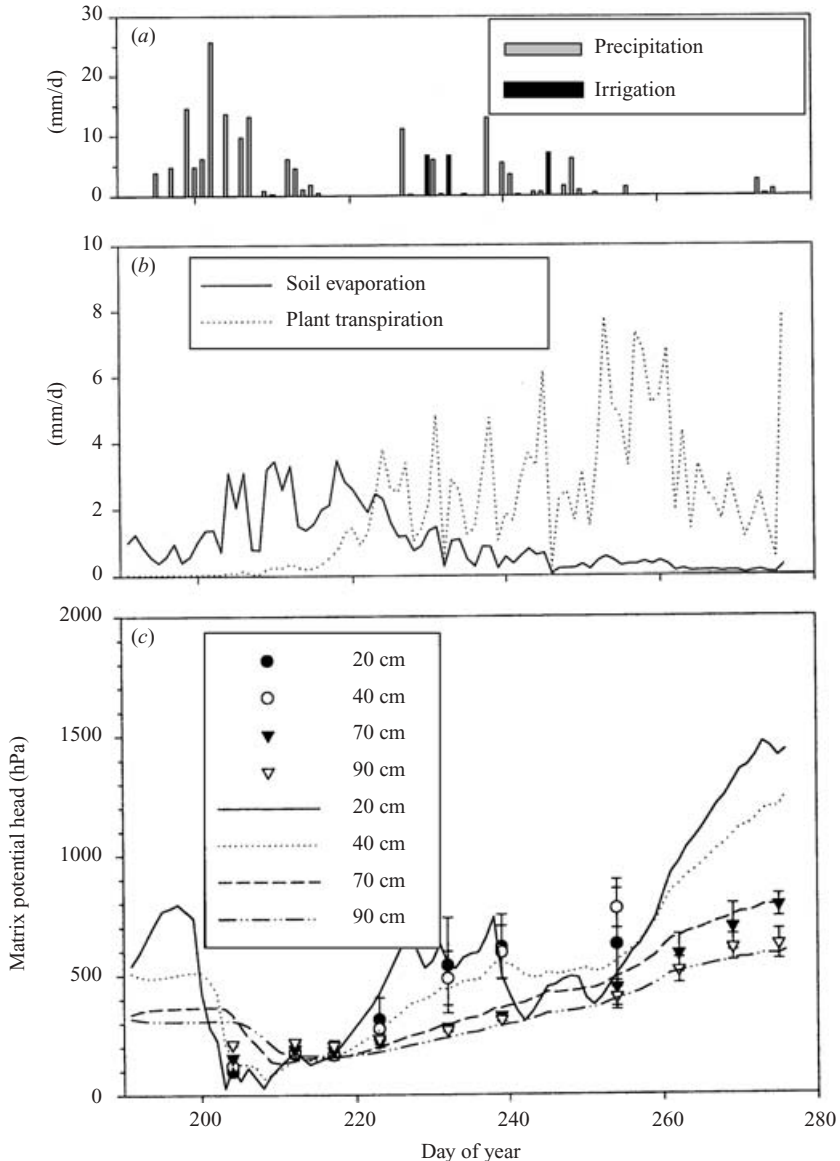
Fig. 2. Precipitation and irrigation during experimental period, calculated soil evaporation and plant transpiration as well as measured and simulated soil matrix potential head in different soil depths from transplanting to last harvest of the optimal fertilized (N2) cauliflower treatment in 1997.

second cauliflower crops, however, clearly higher net mineralization rates were calculated (Table 4).

The *RLD* values of the different N treatments in 1996 (Fig. 2) and 1997 (data not shown) did not differ substantially, despite the indication of a more pronounced root distribution of the N0 treatment in 1996 compared with the N2 treatment. This indicates that the fraction of dry matter allocated to the fine root fraction was elevated under nitrogen deficiency. The

parameter f_{fRmax} (Eqn 5) was estimated by adjustment to the 1996 data at a value of 0·201 ($\pm$0·004). This was the only parameter specifically adjusted using data from the present experiments. Using this parameter value the *RLD* data of the N deficient treatments N0 and N1 in 1996 could be described in a way that the simulated distribution of the root length density was within the standard deviation of the measurements of this parameter (Fig. 2). Also, the

Table 5. *Parameters of a linear regression analysis between measured and simulated soil water tensions* (hPa) *as well as residual mean square error* (RMSE) *and modelling efficiency* (EF). *Data are from the 1997 annual experiment and from the early planted crops of the long-term experiment*

Soil depth (cm)	Slope	Intercept	R^2	n	RMSE	EF
20	1·1724	− 58·1560	0·6214	38	106·8452	0·5962
40	2·5354	− 278·7340	0·5753	38	99·8982	0·3637
70	1·9471	− 155·0777	0·3509	38	66·0248	0·1525

Table 6. *Parameters of a linear regression analysis between measured and simulated soil nitrate nitrogen in different soil layers as well as residual mean square error* (RMSE) *and modelling efficiency* (EF). *Data are from the 1996 and 1997 annual experiments and from the early plantings of the long-term experiment*

Soil depth (cm)	Slope	Intercept	R^2	n	RMSE	EF
0–30	0·9819	5·8324	0·9336	47	28·0339	0·9319
30–60	0·5309	5·8549	0·4380	47	12·2148	0·0251
60–90	1·1340	0·0772	0·7274	47	3·5219	0·6855
90–120	1·0726	0·2127	0·7670	47	3·8381	0·7499
0–120	0·9575	8·4942	0·9303	47	32·0057	0·9278

prediction for the 1997 data was acceptable, with some minor discrepancies between simulated and measured values for the somewhat deeper distributed root system of the N0 treatment (data not shown).

The high amount of rainfall at the beginning of the experiment in 1997 (Fig. 2*a*) lowered the soil water potential down to values close to field capacity up to a soil depth of 90 cm (Fig. 2*c*). Due to soil evaporation and plant transpiration (Fig. 2*b*) the simulated absolute values of soil water potential rises to about 1500 hPa in the topsoil but remained at about 700 hPa in the subsoil. For the other evaluated crops a sufficient description of soil water tensions was also achieved (Table 5).

The soil nitrate content in 1996 changed substantially only in the upper 30 cm of the profile, where the fertilized nitrogen was exhausted rapidly after onset of plant nitrogen uptake (Fig. 3). Due to the low N contents of the deeper soil layers and the absence of leaching during the 1996 vegetation period, changes of soil nitrate in deeper soil layers (> 30 cm) were small. The excess of rainfall at around the 210th day of the year (DOY 210) in 1997 (Fig. 2*a*) induced downward water movement, which transported some nitrate nitrogen from the upper 30 cm of the soil profile to the layer 30–60 cm (Fig. 4). However, due to the high water capacity of the loess loam this leaching process did not affect soil nitrate contents below a depth of 60 cm (Fig. 4). With the exception of the N3 treatment the soil mineral N content was exhausted down to values less than 50 kg N during the growing period. Simulated and measured values for the different soil layers also agreed sufficiently well for the other evaluated crops (Table 6).

The stimulated N uptake rates of the N2 and N3 treatments were, during the time of highest N demand, above 8 kg N/ha per day (1996: Fig. 5; 1997: data not shown). However, due to the high N amounts (Fig. 3) in the comparably dense rooted topsoil (Fig. 1), calculated maximum nitrate transport rates to the root system were always (N3) or until a few days before

final harvest (N2) higher than calculated N uptake. This indicates unrestricted (N3 treatment) or almost unrestricted (N2) N availability for the crops. The suboptimal (N2) and unfertilized (N0) treatments, however, were calculated to be limited in N uptake by N availability in the second half of the growing period (N1) or throughout the growing period (N0) (Fig. 5). The N1 treatment was calculated to be N limited from DOY 210 on wards at a soil nitrate content 0–60 cm of 67 kg N/ha. Hereby an active uptake period of 10 days was assumed (Eqn 1). Assuming an unrestricted uptake period of the roots, however, indicated an N limitation on DOY 218 at a soil mineral N content of 18 kg N/ha (Fig. 5).

The computed apparent mass flow rates were close to the calculated plant uptake rate for the first half of the growing period in the case of the super optimal fertilized N3 treatment. For all other treatments actual N uptake rates were generally much lower than calculated apparent mass flow rates (Fig. 5). Average nitrogen influx rates show an initial phase of increase shortly after planting, but steadily decrease thereafter. Peak values are higher than $5/10^{12}$ mol N/cm per second if calculated using total root length and about $15/10^{12}$ mol N/cm per second if calculated using an 'effective' root length (Fig. 6).

A scenario calculation was carried out for the N2 treatments of both years using the soil hydraulic parameters of a sandy soil instead of the parameters for the loess soil (Table 2). All other input values were left unchanged. Due to the lower water capacity of this soil type the calculated downward movement of nitrate during the vegetation periods of both years was more pronounced than was measured and simulated at the loess loam location (Figs 3 and 4 *v.* Fig. 7). But the rainfall-induced downward movement of water and nitrate was limited to a soil depth of about 60 cm. This limited translocation of nitrate, however, increased the amount of unused soil mineral nitrogen left in the soil at 30–60 cm compared with the loess
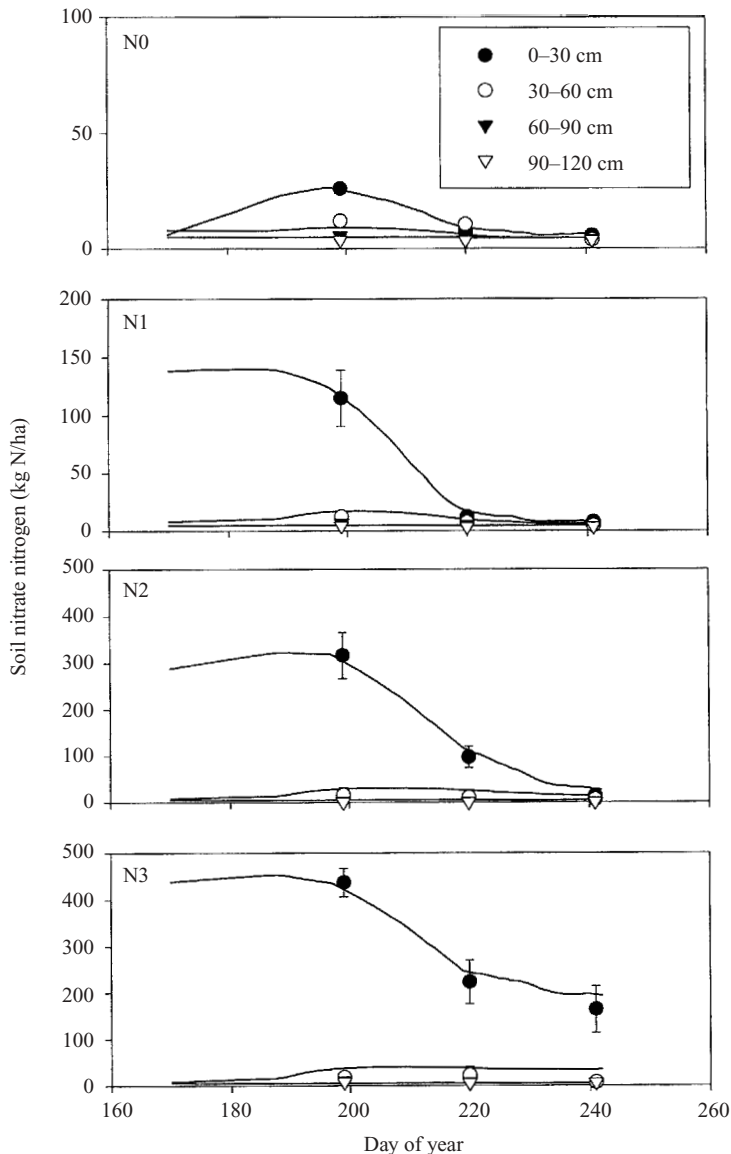
Fig. 3. Measured and simulated soil mineral nitrogen content of the 1996 cauliflower experiment of the 4 N treatments. Error bars indicate the standard error of the mean.

loam soil conditions, especially under 1997 weather conditions (Fig. 7).

A further scenario calculation was carried out to obtain response curves of residual soil nitrate at harvest from 0–120 cm soil depth to N fertilization. Again, two different sets of hydraulic parameters were used, the parameter set for the loess soil of the experimental field and another of a sandy soil (Table 2). On the sandy soils possible effects of a split nitrogen application were also evaluated assuming a fixed nitrogen application at planting of 100 kg N/ha and varied

secondary application 4 weeks after planting. For N mineralization rate the same values as shown in Table 3 for the N2 treatment in 1997 were used.

Residual soil nitrate values remain at low values of about 20 kg N/ha up to a N fertilization of about 200 kg N/ha for the loess loam soil conditions and about 50 kg N/ha up to 150 kg N/ha fertilization for the standy soil (Fig. 8). Split nitrogen application on the sandy soil is calculated to delay the increase of residual soil nitrate towards a higher level of N supply. Starting at an N fertilization of about 250 kg N/ha,
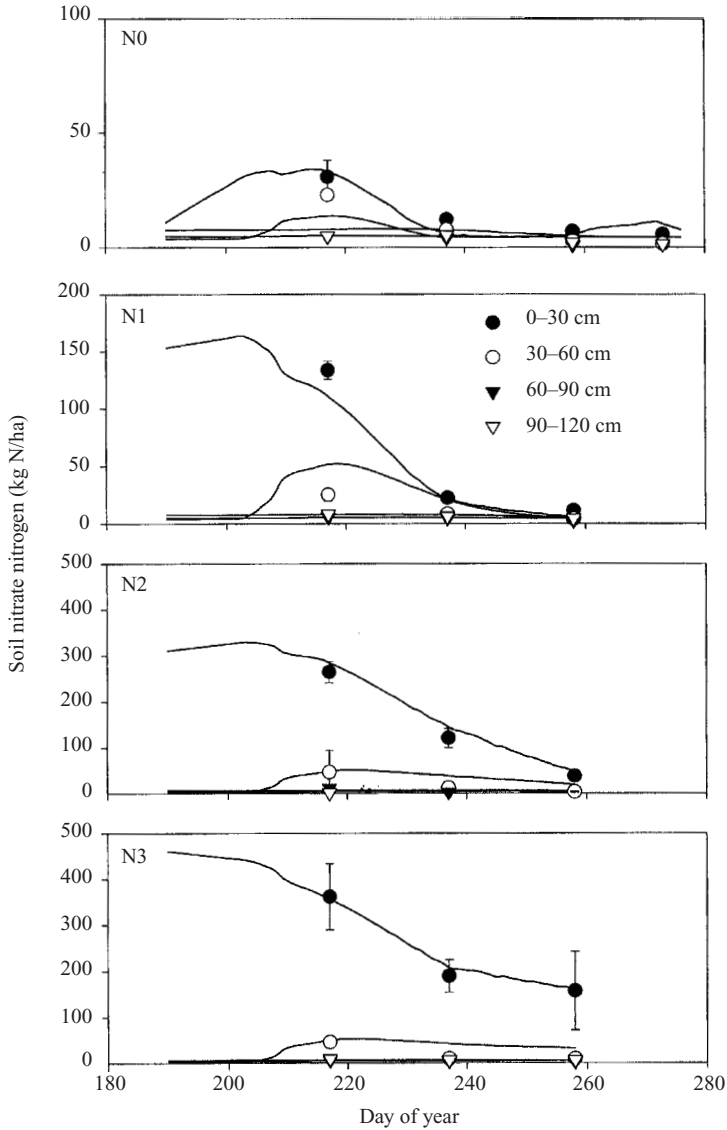
Fig. 4. Measured and simulated soil material nitrogen content of the 1997 cauliflower experiment of the 4 N treatments. Error bars indicate the standard error of the mean.

the sink capacity of the cauliflower is saturated and residual soil nitrate levels are increasing linearly for all conditions considered in the calculation.

DISCUSSION

The aim of the present work was to quantify the nitrogen availability for cauliflower crops grown under different nitrogen supplies using a mechanistic simulation model. Furthermore scenario calculations were carried out to estimate effects of altered soil conditions.

The adapted root growth module from Kage *et al.* (2000) sufficiently described the temporo-spatial pattern of root length density (Fig. 1). The discrepancy of measured and simulated *RLD* in 75–90 cm depth of the N0 treatment in the annual experiment of 1996, however, indicates that even small amounts of nitrogen in the sub soil (Fig. 3) may induce local deviations of the root profile from the negative exponential shape predicted by the model if nitrogen is deficient. Such 'irregular' root growth patterns may be much more severe if roots of N deficient plants tap into sub soil regions with high N nitrate concentrations (Drew
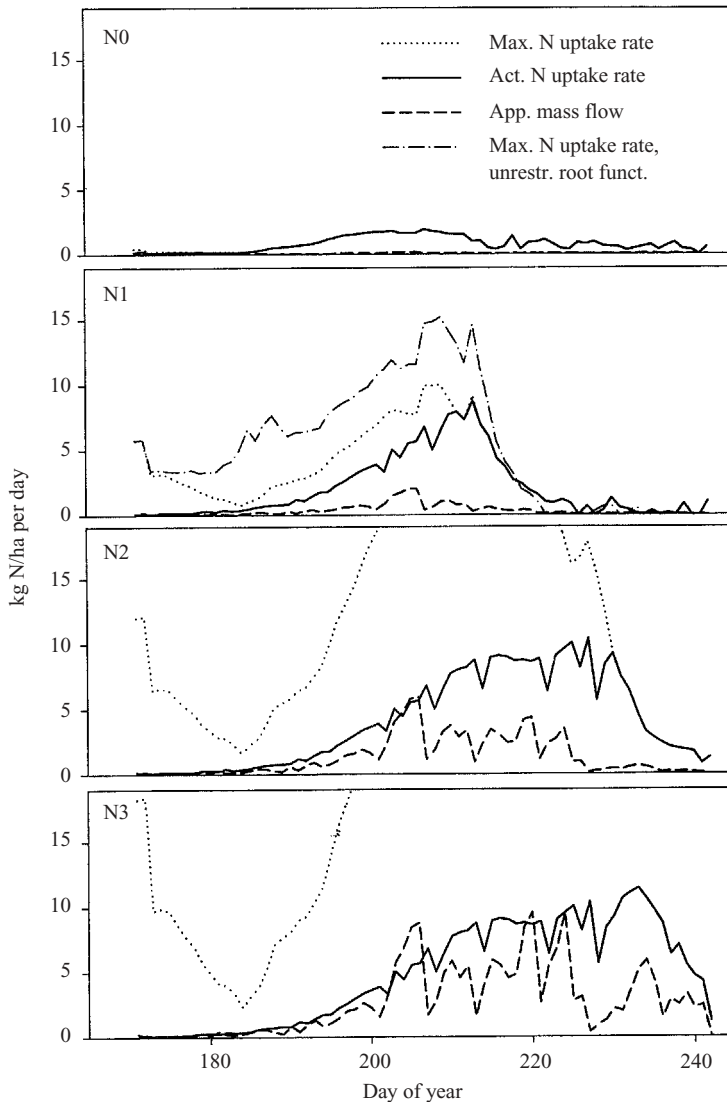
Fig. 5. Simulated maximum nitrate transport rates to the root system, apparent mass flow and actual N uptake rates of cauliflower from the 1996 experiment for 4 different N treatments.

& Saker 1975; Burns 1991). The approach taken in the present paper to account for a changing assimilate partitioning between roots and shoots under nitrogen deficiency (Eqn 5) accurately described the data obtained (Fig. 2) even under a quite extreme variation of N supply. But it may fail to predict responses of rooting intensity under different soil conditions, because the beneficial effect of an increased root growth on N uptake depends clearly on particular soil conditions such as water content and the vertical distribution of nitrate in the soil profile. Teleonomic approaches, explaining shoot-root partitioning with

growth maximizing principles (Thornley 1972; Johnson & Thornley 1987; Kleemola *et al.* 1996) may be superior for this purpose. However, their elaboration and parameterization calls for more detailed data than those which were available in the present study.

The good agreement between simulated and measured soil nitrate in different soil layers (Figs 3 and 4) is mainly due to the good description of the time course of crop nitrogen uptake by the model modules presented in the second part of this work because net mineralization was input and downward movement of nitrate was, even in 1997, of limited
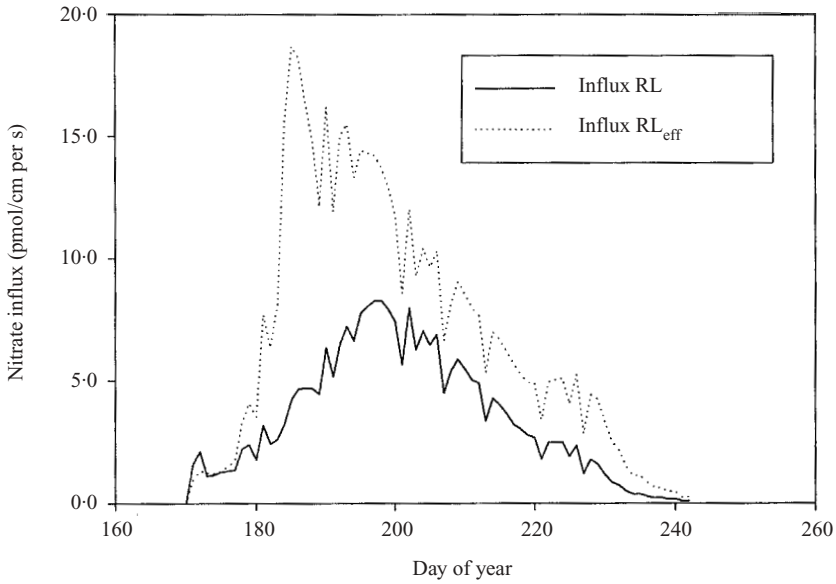
Fig. 6. Calculated N influx (N uptake per units root length) using either simulated total (RL) or effective root length (RL$_{eff}$) for the N2 treatment of the 1996 annual experiment.
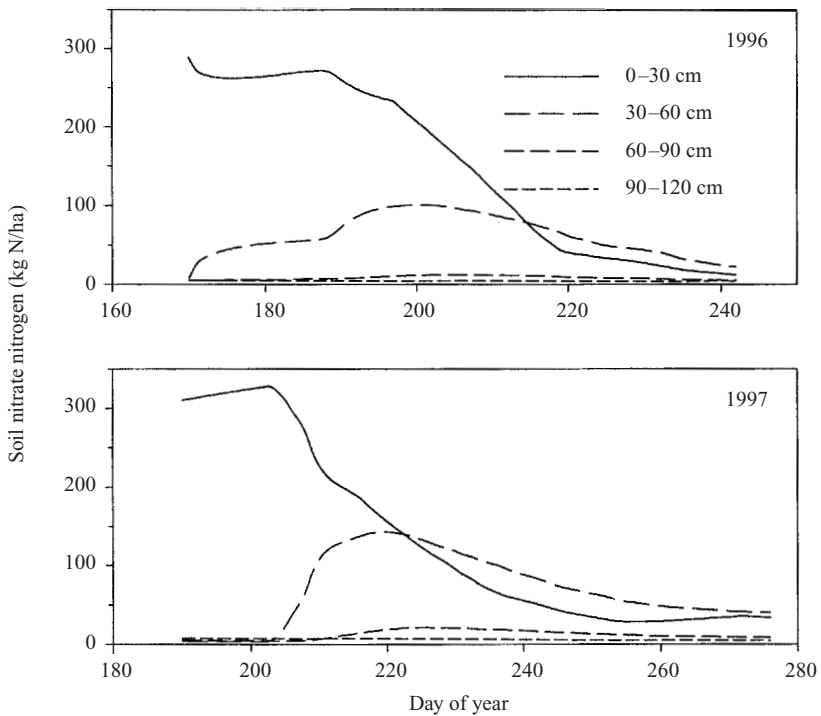

Fig. 7. Simulated soil nitrate content in different layers for a scenario calculation using soil hydraulic parameters of a sandy soil for the N2 treatments of the 1996 and 1997 experiments.
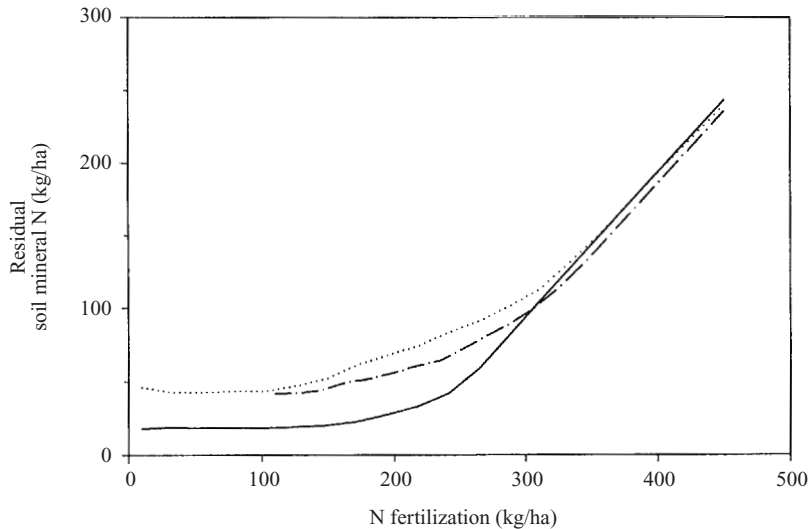
Fig. 8. Residual soil nitrate from 0–120 cm under varying nitrogen fertilization rates for a loess loam soil, a sandy soil and a sandy soil with split N application. All other input variables as in the 1997 annual experiment (—, loess loam soil; ......, sandy soil; —·—·—, sandy soil with split nitrogen application).

importance for soil nitrogen dynamics (Fig. 4). As shown in Tables 3 and 4 there is a substantial variation of net mineralization depending presumably on seasonal variations of soil temperature, the preceding crop (Greenwood *et al.* 1996) and the amount of N fertilization (Blankenau & Kuhlmann 2000).

The calculation presented in Fig. 5 clearly demonstrates that mass flow is only able to contribute substantially to the nitrate transport to roots if the soil nitrate concentration is very high, as already stated by Strebel & Duynisveld (1989) and Kage (1996). The estimated nitrate influx rates for the whole root system are about one order of magnitude higher than values reported for winter wheat (Barraclough 1986; Robinson *et al.* 1994) and winter rape (Barraclough 1989). This is due to an additive effect of higher nitrogen uptake rates of cauliflower per unit of ground area (Fig. 6) and a lower total root length (Kage *et al.* 2000) compared with both agricultural crops mentioned above. Influx rates are almost doubled for the calculated effective root length. These high influx values are the prerequisite for the reproduction of the high critical soil nitrate values found in the field (Alt *et al.* 2000) by the single root model.

The scenario calculation for the sandy soil (Figs 7 and 8) indicates that even for this soil type leaching losses of nitrogen out of the root zone during the growing period of cauliflower are limited. However, it has to be stated that at the beginning of the growing period nitrate nitrogen was situated predominantly in the upper 30 cm of the soil in both years. But even the limited calculated downward movement of nitrate lowers the availability because of the lower rooting

density in the sub soil (Fig. 1), resulting in somewhat increased residual soil nitrate level in the 30–60 cm layer (Fig. 7). Due to the different water content–soil water potential characteristic of the sandy soil the calculated water contents are lower in the sandy soil compared with the loess loam. This also reduces nitrate availability because nitrate diffusion is closely dependent on the soil water content. Critical soil nitrate levels and consequently residual soil nitrate levels are therefore higher for sandy soils than for loamy soils (Fig. 8). For both soil types residual soil nitrogen values are increasing only after the N uptake capacity of the cauliflower crop is reached. This behaviour has also been found for other crops like winter wheat (Chaney 1990).

The postulation of a limited active duration of root functioning used in the present study is a very crude approach to bridge the gap between observed critical soil nitrate concentrations (Alt *et al.* 2000) and the predictions obtained using an unrestricted functional time of roots (Fig. 5). The estimation of this active duration by adjustment with respect to measured and simulated critical soil nitrate values lumps the effects of all unrealistic simplifications of the model into one causal factor. Consequently, a presumably much too low value of a 10-day period of N uptake was found to give an acceptable prediction of critical soil nitrogen content (Figs 3 and 5). Other candidates for explaining elevated predictions of the model for maximum nitrate uptake rates of the root system are: (a) horizontally uneven root distribution (Baldwin *et al.* 1972; De Willigen & Van Noordwijk 1987*b*; Kage 1992; Droogers *et al.* 1997), (b) limited soil–root contact

(Herkelrath *et al.* 1977; De Willigen & Van Noord-wijk 1987*a*), (c) locally decreased soil water contents around water-absorbing roots (Herkelrath *et al.* 1977; Hainsworth & Aylmore 1986; Kage & Ehlers 1996), (d) horizontally uneven distribution of soil nitrate (Van Noordwijk & Wadman 1992; Hodge *et al.* 1999). The incorporation of these effects into the model may reduce the contradiction between the functional time of roots in the model and physiologically realistic values, but would also increase the number of un-known and hardly measurable model parameters. The approach of an effective root length presented here may therefore be regarded as acceptable, since it pre-serves the mechanistic character of the single root model approach and may therefore give realistic pre-dictions even when extrapolated to other experimental conditions. However, it also clearly focuses the knowl-edge gap between empirically determined critical soil nitrogen contents and the prediction of mathematical models of root functioning.

CONCLUSIONS

Root growth of cauliflower under nitrogen deficiency could be described as increasing the fraction of dry matter allocated to the fine root fraction. Rooting depth and vertical root distribution were obviously not severely affected. A mechanistic model of nitrate availability calculated lower critical soil nitrogen contents than were empirically derived. Critical soil nitrate values may be higher for sandy than for soils with a higher water-holding capacity.

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