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Modelling ammonium and nitrate uptake by a mature Douglas-fir stand from a soil with high atmospheric NH_x input

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Abstract

Model calculations were performed on N uptake by 40-year-old Douglas-fir trees from a sandy soil situated in an area with a high NH_x input level. Two model approaches were applied to distribute N uptake over the root system and over the two N sources, ammonium and nitrate. In the first approach, priority was given to maximizing the relative ammonium contribution to N uptake; the other approach aimed at a uniform N uptake rate for all roots. Total N uptake was the same with both approaches, but the distribution of N uptake over roots in various layers was different, as was also the contribution of ammonium to total-N uptake. During a large part of the growing season the amount of N that could be taken up by the roots was lower than the N demand of the trees. Ammonium accounted for at least one quarter and at most about half of the amount of N taken up by the trees, which uncertainty resulted from the different model approaches used and from variability in input data. Large differences in relative ammonium contribution to N uptake existed among roots in various soil layers. In the upper soil layers, the ammonium contribution was considerable during a large part of the growing season, so acidification of the rhizosphere may be expected. In deeper layers, mainly nitrate was taken up, so the rhizosphere will be alkalized. Possible effects of changes in NH_x input level, nitrification rate and tree growth on N uptake are discussed.

Keywords: nitrification, N transport through the soil, N uptake, proton excretion, *Pseudotsuga menziesii*, rhizosphere pH, soil acidification

Introduction

Most Dutch coniferous woodlands are situated on strongly acid sandy soils in areas with high levels of atmospheric NH_x (i.e. $NH_3 + NH_4^+$) deposition. For interpreting the effect of this deposition on forests, it is important to know in what form nitrogen is taken up by the trees. It was shown earlier that Douglas-fir on acid soil may show poor growth (Gijsman, 1990b) and high mortality (Smit et al., 1987; Gijsman, 1990b), when it takes up N mainly in the ammonium form. This may be due to physiological disorders – like high arginine tissue concentrations (van Dijk & Roelofs, 1988) or low carboxylate tissue concentrations (Gijsman, 1990b) – or to acidification of the rhizosphere (Gijsman, 1990a; 1990c, 1991).

The rate at which ammonium and nitrate are taken up by the roots depends on the supply of either N source at the soil/root interface, the N requirement of the plant and the uptake preference of the plant for ammonium or nitrate. In the soil solution of various soil layers, a mixture of ammonium and nitrate at different concentrations and at different concentration ratios is available to the roots. The N uptake pattern of roots in various soil layers, therefore, may be completely different. In an earlier paper (Gijsman, 1991), it was shown that Douglas-fir takes up ammonium preferentially above nitrate from a sandy soil. It is, however, not clear whether this ammonium preference is absolute or whether still a certain amount of nitrate is taken up, even if ammonium supply is sufficient to meet N demand (cf. Keltjens & van Loenen, 1989; Kamminga-van Wijk, in prep.).

In order to examine whether adverse conditions due to high ammonium uptake are likely to exist in Dutch Douglas-fir forests, calculations were performed on the uptake of ammonium and nitrate from a sandy forest soil. Use was made of a simulation model on nutrient transport through the soil towards the roots and nutrient uptake by these roots. Two different approaches on the distribution of N uptake over the root system were used: one based on ammonium preference at total-tree level, the other based on ammonium preference at the level of individual soil layers. Input data for a specific forest research site were made available by several colleagues working in the Dutch Priority Programme on Acidification. From the point of view of acidification research and policy, it is interesting to see what the effect on N uptake is of changes in the level of NH_x input to the soil, changes in the rate of nitrification of the NH_x deposited, or changes in tree growth rate. Therefore, these situations were also examined.

Description of the model and the input parameters

Simulation model

The simulation model used is a numerical model, based upon analytical solutions of transport and uptake equations. The mathematical theory was described by de Willigen & van Noordwijk (1987; in prep.). Nitrogen transport through the soil towards the roots is described by diffusion and mass flow. Nitrogen uptake is considered to be determined principally by the plant's N demand, independent of the N concentration in the soil. This implies that roots take up N at the required rate (i.e. in accordance with the plant's N demand) as long as the supply of N at the root surface is sufficient to meet the N demand. This situation is called an 'unconstrained uptake pattern'. When the N demand is higher than the rate of N supply at the root surface, the roots will take up all N reaching the root surface, thus acting as a zero sink ('constrained uptake pattern'). The N transport rate towards a root due to mass flow and the N uptake rate by a root have upper bounds, which are determined by the maximum fluxes across the root surface of water and N, respectively.

The N demand is defined as the amount of N needed to be taken up by the trees (per unit of time and per unit of soil surface area) for obtaining maximum growth rate under the given other external conditions (thus with regards to e.g. availability of other nutrients and water). It is based on maximum (but still non-toxic) N tissue concentrations. The N demand divided by the total root length per unit soil surface area gives the required N uptake rate per unit root length.

The roots are considered as regularly distributed, parallel vertical cylinders, each surrounded by a hexagonal block of soil, which can be approximated by a soil cylinder with radius R (in cm):

$$R = 1/\sqrt{(\pi L_{rv})}, \tag{1}$$

in which L_{rv} stands for the root length density (cm cm^{-3}).

It is assumed that the flux of water around the root is distributed according to a steady-state situation with replenishment at the outer boundary of the soil cylinder. The rate of replenishment equals the uptake rate of water.

The soil profile is divided into horizontal layers, each with its own input parameters on root length density, N concentration and water content. It is assumed that there is no exchange of water or nitrogen between different layers; the soil water content and N concentration of each layer and the water extraction rate from that layer are set as forcing functions. They are defined at bulk soil level. The development of gradients in soil water content and N concentration around a root is implicitely included in the mathematical transport equations.

Given a certain required N uptake rate per unit root length, it is calculated whether roots in a certain layer are able to take up according to an unconstrained uptake pattern. If not, the maximum uptake rate from that layer is calculated as it is determined by the potential N transport from the bulk soil towards the root surface (constrained uptake). This calculation is performed for each soil layer. If roots in a certain layer cannot meet the uptake requirement, it is tested whether roots in other layers (not yet taking up at their maximum rate) can increase their uptake rate. This procedure is repeated until the N demand can be met or until all roots are taking up at their maximum rate, the latter implying that all N reaching the root surface is taken up or that N uptake rate is limited by physiological limits. The uptake routine which forms the pivot on which the model hinges was published by de Willigen (1990).

When modelling N uptake for both ammonium and nitrate concurrently at the same time, the N demand has to be distributed not only over the root system, but also over the two N sources. Then an important uncertainty is the possibility of uptake interaction between the two N sources and between different root zones having different N supply. With the starting point of an (absolute) preference of Douglas-fir for uptake of ammonium above nitrate, two extreme approaches can be made:

1. Priority is given in the calculations to fulfilling the N demand of the tree primarily by ammonium uptake, irrespective the soil layer where it comes from. If ammonium availability in the total soil profile is insufficient to meet the N demand, the remainder is met by nitrate uptake (if enough nitrate is available). As a consequence of this approach, the presence of a few soil layers very rich in ammonium, may lead to total fulfilment of the N demand by NH_4^+ uptake from those layers. Roots in other layers then will not participate in N uptake at all, not even

when they are growing in a layer with a huge amount of available nitrate. With this approach, therefore, the maximum possible ammonium uptake of the whole tree is calculated. It will be referred to as the 'approach with priority to ammonium uptake'.

2. Priority is given in the calculations to a homogeneous distribution of the N uptake of the tree over all roots; the question of ammonium preference is only of interest within each soil layer separately. Now, roots in an ammonium-rich layer will take up mainly ammonium, while roots in a nitrate-rich (but ammonium-poor) layer will take up mainly nitrate. If both N sources are available in the same layer at the same time, the ammonium preference will lead to fulfilment of the N requirement of roots in this layer as far as possible by ammonium uptake. With this approach the total-N uptake rate of the tree will be the same as calculated by the first approach, but the amount of ammonium taken up will be smaller. Moreover, all roots will now participate in N uptake. This will be referred to as the 'approach with priority to uniform N uptake'.

Input parameters

All calculations were performed with input parameters measured at the forest research site of the Dutch Priority Programme on Acidification (ACIFORN site) at Kootwijk, the Netherlands. This forest is an about 40-year-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) monoculture, situated on a sandy soil.

For calculations, the soil was divided into a 2-cm humus top layer, followed by ten layers of 10 cm each and a bottom layer of 25 cm. Total profile depth thus is 127 cm.

The (fine) root length density at various soil depths was determined in May 1988 by means of root sampling with an auger (Figure 1; Olsthoorn, pers. comm.; 1991). Since this sampling date was just after the growth flush in spring, these data represent the yearly maximum in root length density. Additional measurements on root growth dynamics throughout the year with a minirhizotron system, showed that root turn-over rates were at most about 1 yr^{-1} (Olsthoorn & Gijsman; unpublished data), a value also used by Mohren (1987). Since root length densities thus only varied little, the values of May were considered to hold for the entire growing season. To examine the effect of variation in root length densities, calculations were also performed with other values (these are indicated in the text).

The concentrations of ammonium and nitrate in the soil solution were determined once every 14 days. Solutions were collected by means of suction cups or plates, positioned at various soil depths (Figure 2; van der Maas, pers. comm.). Samples were taken during the last three days of the 14-day interval, but this value was considered to hold for the whole interval. Variation in concentration between replicates was very large (with variation coefficients up to 200%), which was probably due to sampling points being near to the stem of a tree, just below a dripping point of a branch or below a gap in the canopy. No information was available on the horizontal distribution of the roots in relation to the variation in N concentration in the soil. Therefore, average values had to be used, assuming horizontal homogene-

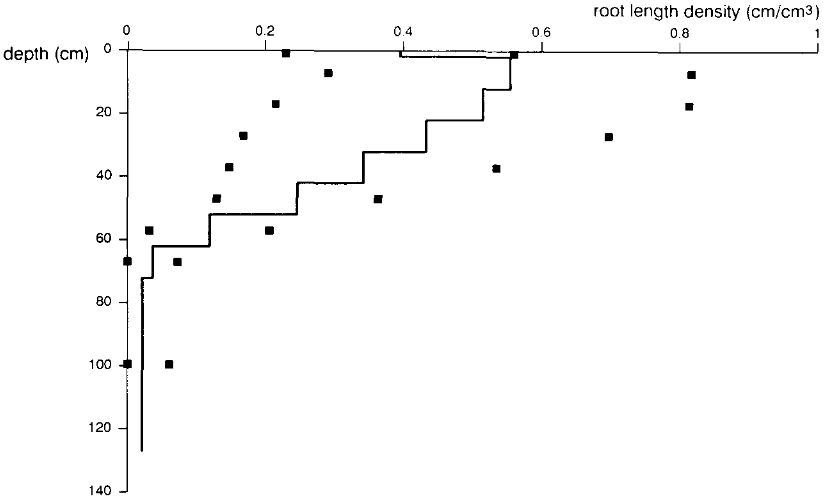

Fig. 1. Root length density (cm cm^{-3}) per soil layer. Mean (line) and mean plus/minus standard deviation (dots), respectively. Data from Olsthoorn (pers. comm.; 1991).

ity. To examine the effect of the variations in N concentration, calculations were also performed with minimum and maximum values.

Soil water content was measured weekly by Tiktak & Bouten (1990), by time-domain reflectometry (Topp et al., 1980) for depths until 50 cm and by the neutron scattering method (Gardner & Kirkham, 1952) for depths between 50 and 260 cm. Soil water pressure heads were automatically recorded by means of tensiometers (Bird, 1978) to depths of 200 cm. From these measurements, soil water content and water extraction rate by the roots were calculated on a daily basis, using the SWIF model (Tiktak & Bouten, 1990). Values were given for the humus layer separately and per 5 cm layer for the rest of the soil profile (Figure 3; Tiktak & Bouten, pers. comm.).

The N demand of the forest (Figure 4; Mohren, pers. comm.) was calculated with a model on forest growth (FORGRO; Mohren, 1987). Results from various on-site measurements at the ACIFORN plot – e.g. data on weather, soil water content, soil nutrient concentrations and canopy structure – were used as input for this growth model to calculate dry matter production of wood, needles and roots. From these, the N demand was calculated using the maximum N concentrations of various plant parts and including the possibility of redistribution of N within the plant.

Other input parameters used in the model are given below:

- The diffusion coefficients for ammonium and nitrate in water (D_l) were 1.45 and 1.39 cm^2 d^{-1}, respectively (Li & Gregory, 1974).
- The relation between volumetric water content of the soil (θ) and tortuosity (f_l) was taken from Barraclough & Tinker (1981) for θ values exceeding 0.15 cm^3 cm^{-3} and from Rowell et al. (1967) for lower θ values; both were measured on a (sandy clay) loam.

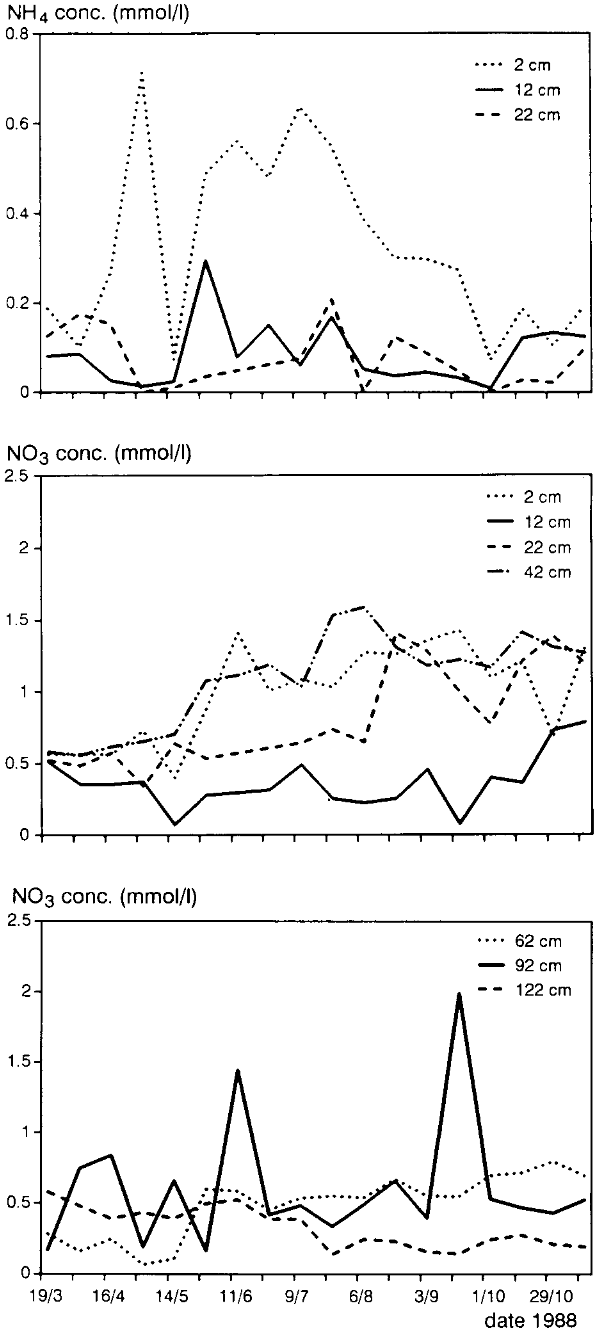

Fig. 2. Mean ammonium and nitrate concentrations (mmol l^{-1}) in the soil solution at various depths (cm). At sampling points below 22 cm depth, ammonium concentrations were very low, so these data are not presented in the figure. Data from van der Maas (pers. comm.).

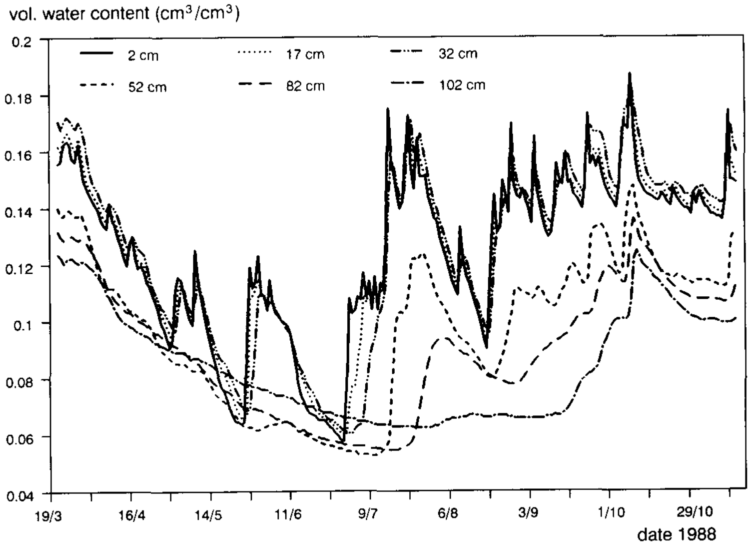

Fig. 3. Volumetric water content of the soil (cm^3 cm^{-3}) at various depths (cm). Data from Tiktak & Bouten (pers. comm.).

- The maximum fluxes of ammonium and nitrate across the root surface were calculated from data on N uptake by seedlings from a nutrient solution (Kamminga-van Wijk, in prep.); these maximum fluxes were about 7×10^{-4} and 4×10^{-4} mmol cm^{-2} d^{-1}, respectively.
- The maximum water flux across the root surface was calculated from a literature review by de Willigen & van Noordwijk (1987) and from data of Kruger & Sucoff (1989); its value was set at 0.44 cm^3 cm^{-2} d^{-1}.

Calculations

Unless stated otherwise, the calculations were performed using average data for various parameters, which will be referred to as 'standard input'. Calculations were also performed for situations of increased NH_x deposition or modified nitrification rate. Since part of the ammonium in the soil is adsorbed onto the soil cation exchange complex, a shift in total ammonium content will only partly be reflected in the ammonium concentration in the soil solution. Therefore, allowance has to be made for the adsorption coefficient K_a, i.e. the ratio of the concentration in the solid soil phase and the concentration in the liquid soil phase. Although its value is not exactly known for the various soil layers, it could be estimated at about 2 cm^3 cm^{-3} (Gijsman, 1991). As with increasing soil acidification, part of the ammonium on the soil complex may be replaced by H^+ or Al^{3+} ions, leading to a lower K_a for ammonium, calculations were also performed for $K_a = 0$ cm^3 cm^{-3}.

Results

Total-N uptake rate

Using the standard input, it was calculated (Figure 4) that early in the season the N uptake rate of the roots could meet the N demand (unconstrained uptake). From the end of April until mid-July, however, the soil could not provide the roots with enough N to meet the N demand (constrained uptake). From mid-July until the end of the growing season, N availability again was sufficiently high. The total amount of N taken up during the whole growing season was calculated at about 61 kg ha^{-1}; cumulative N demand amounted to about 105 kg ha^{-1}.

The maximum N uptake rate that probably could be reached was calculated using the measured maximum N concentrations in the soil instead of the average data, and increasing the root density by one standard deviation. Then the N uptake rate evidently was higher during the period of constrained uptake, the duration of this period was reduced and it was interrupted by a two-week period in early June during which the N demand could be completely met by N uptake. Calculated N uptake during the whole growing season in this situation was about 79 kg ha^{-1}.

Contribution of ammonium to N uptake

The relative contribution of ammonium to N uptake was calculated according to the 'approach with priority to ammonium uptake' and the 'approach with priority to

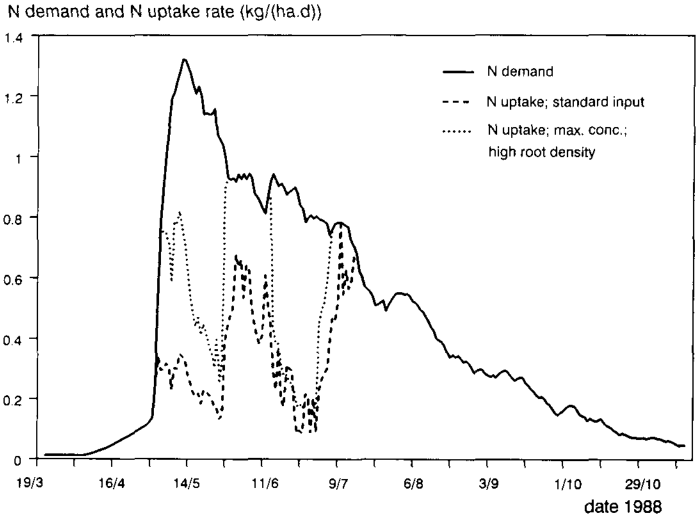

Fig. 4. Calculated N demand of the forest (kg ha^{-1} d^{-1}; data from Mohren, pers. comm.) and N uptake rate integrated over the total soil profile (kg ha^{-1} d^{-1}), as calculated with standard input or with maximum ammonium and nitrate concentations and a root density increased by one standard deviation.

uniform N uptake'. Differences in results between the two approaches were only expected in the period during which N uptake rate was equal to N demand, since otherwise roots were taking up all N reaching the root surface.

Figure 5 shows that, with the first approach, the relative contribution of ammonium to N uptake rate was small during the larger part of the growing season. In early spring and during autumn, the plants could meet their N demand (almost) completely with ammonium. The sudden increase in relative ammonium contribution in early/mid July can be explained by an increase in soil water content due to a few showers. Integrated over the whole growing season, ammonium contributed about 27 % to total-N uptake.

With the 'approach with priority to uniform N uptake', the relative contribution of ammonium to N uptake was small in spring and autumn, but it was almost the same in the intermediate period. Integrated over the whole growing season about 24 % of the N was taken up as ammonium.

A much larger difference between the two model approaches existed in the results on N uptake rate from individual layers and the relative contribution of ammonium to N uptake within a certain soil layer. With the 'approach with priority to ammonium uptake', most nitrogen was taken up in the ammonium-rich (top) layers during the period of unconstrained uptake, while roots in deeper soil layers only slightly contributed to N uptake (Figure 6). With the 'approach with priority to uniform N uptake', roots in all layers participated in N uptake as much as possible at equal rate (per unit root length), resulting in a relatively higher uptake rate in deeper soil layers. As a result of this shift in N uptake pattern, the fraction of N taken up

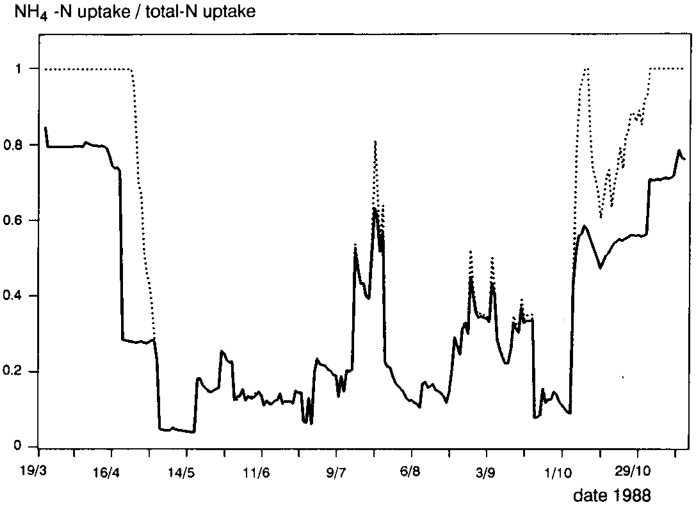

Fig. 5. Relative contribution of NH_4-N to total-N uptake rate integrated over the whole soil profile, as calculated with the 'approach with priority to ammonium uptake' (dots) and the 'approach with priority to uniform N uptake' (line). Standard input.

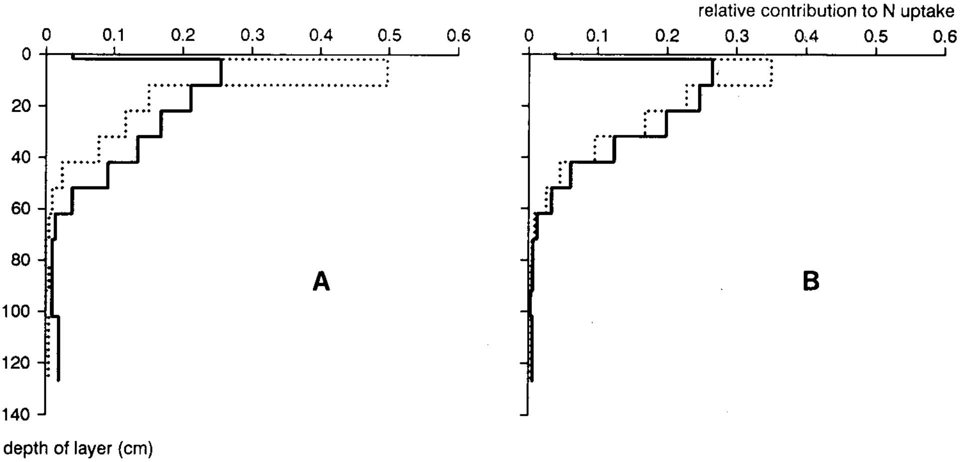

Fig. 6. Relative contribution of N uptake per soil layer to N uptake integrated over the whole soil profile, as calculated with the 'approach with priority to ammonium uptake' (dots) and the 'approach with priority to uniform N uptake' (line). A = first period of unconstrained uptake (i.e. 22/3-2/5); B = second period of unconstrained uptake (i.e. 16/7-15/11).

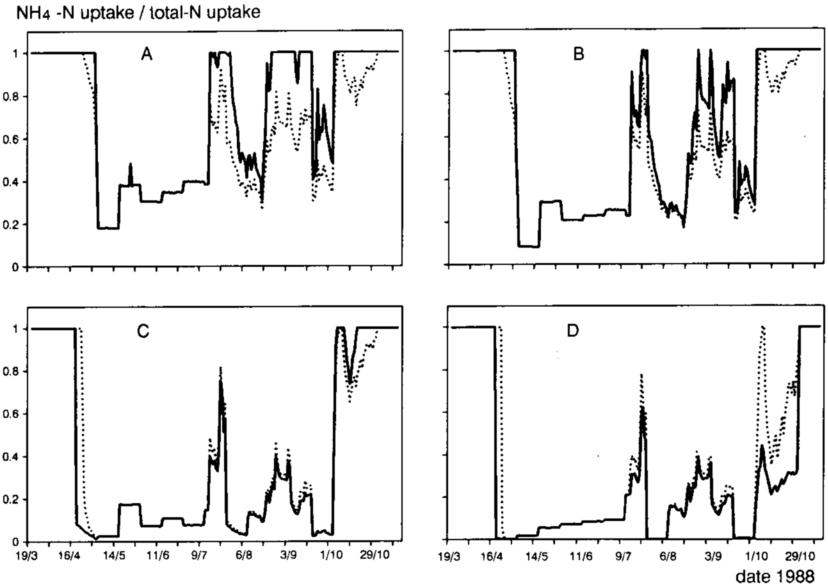

Fig. 7. Relative contribution of NH_4-N to total-N uptake rate per soil layer for the upper four layers, as calculated with the 'approach with priority to ammonium uptake' (dots) and the 'approach with priority to uniform N uptake' (line). A, B, C, D = layer 1, 2, 3, 4, respectively. Standard input.

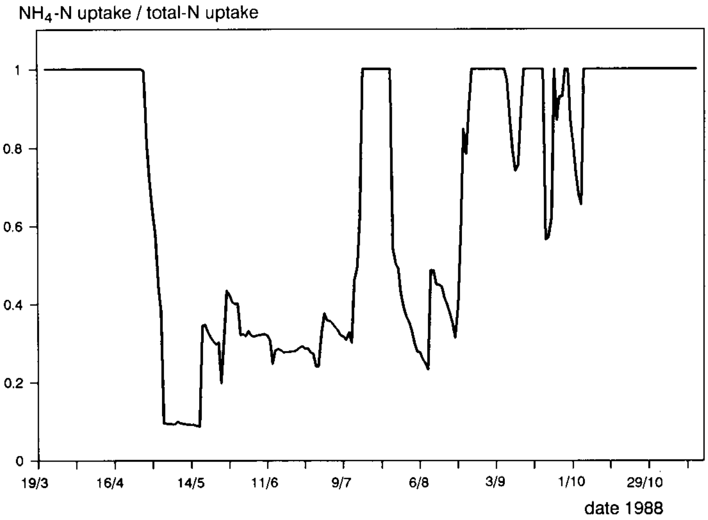

Fig. 8. Relative contribution of NH_4-N to total-N uptake rate integrated over the whole soil profile, as calculated with maximum ammonium and minimum nitrate concentrations and a root density increased by one standard deviation.

as ammonium for each individual layer was higher in the top layers (Figure 7A,B) and lower in the deeper layers (Figure 7D) when the second approach was used (Figure 7C is intermediate, depending on the time of the year).

The maximum possible ammonium contribution to N uptake was determined by using the maximum measured ammonium concentration in each layer combined with the minimum measured nitrate concentration and a root density that was increased by one standard deviation ('approach with priority to ammonium uptake'). Now, the fraction of N taken up as ammonium integrated over the whole growing season increased to about 56 %, while during late summer and autumn ammonium uptake strongly prevailed over nitrate uptake (Figure 8).

When examining whether adverse conditions due to ammonium nutrition are likely to occur, the maximum possible ammonium contribution to total-N uptake is the important datum. Further calculations on the effect of changes in the soil/plant system on N uptake were therefore only performed with the 'approach with priority to ammonium uptake'.

Effect of increased atmospheric NH_x input

Increased NH_x input into the soil will at first lead to a higher ammonium concentration in the top soil, but in the longer term N concentration in the whole soil profile will increase. This situation was simulated by assuming (1) a 20 % increase in the ammonium concentration in the upper three soil layers or (2) a 20 % increase in both ammonium and nitrate concentrations in the whole profile. Note that the in-

Table 1. Calculated N uptake and NH_4-N uptake (kg ha^{-1}) during the growing season, as affected by changes in the ammonium and nitrate concentrations in the soil solution. For explanation of the treatments see text. Calculations in the lower part of the table were done with K_a = 0 and 2 cm^3 cm^{-3}, respectively.

Treatment	N uptake		NH_4-N uptake		NH_4-N uptake/ N uptake	
Standard input	61.0		16.6		0.27	
20 % extra NH_4 (layer 1-3)	61.6		19.1		0.31	
20 % extra (NH_4 + NO_3) (total profile)	65.6		19.4		0.30	
	K_a =		K_a =		K_a =	
	0	*2*	*0*	*2*	*0*	*2*
20 % $NH_4 \rightarrow NO_3$ (layer 1-3)	60.9	61.7	14.0	14.0	0.23	0.23
20 % $NO_3 \rightarrow NH_4$ (layer 1-3)	61.0	59.5	31.8	24.5	0.52	0.41

crease in total amount of N in the soil solution was greater in the latter situation.

Increasing the ammonium concentration in the upper three layers barely affects total-N uptake rate, while ammonium uptake rate is slightly increased (Table 1). A higher total-N level of the whole profile, on the other hand, leads to an increased total-N uptake rate during the period of constrained uptake, giving an additional annual N uptake of 4.6 kg ha^{-1}. The ammonium contribution to N uptake slightly increases.

Effect of a change in nitrification rate

A change in nitrification rate was simulated by converting 20 % of the ammonium in the upper three layers into nitrate ('increased nitrification') or converting 20 % of the nitrate in the upper three layers into ammonium ('reduced nitrification'). The total amount of N in the soil remained the same. The effect of these changes on N concentration in the soil solution largely depends on the ammonium adsorption coefficient. Calculations were performed with K_a values of 0 and 2 cm^3 cm^{-3}, respectively.

Converting part of the ammonium into nitrate does not affect total-N uptake if K_a = 0 cm^3 cm^{-3} (Table 1), since the total amount of N in the soil solution remains the same. If K_a = 2 cm^3 cm^{-3}, part of the ammonium present in the soil is adsorbed onto the soil cation exchange complex; conversion of 20 % of the ammonium into nitrate results in an increase in total-N concentration in the soil solution. This, however, is barely reflected in a higher N uptake. With both K_a values the ammonium concentration in the soil solution is reduced by 20 %, so ammonium uptake is equal in both situations; it is lower than in the standard situation. The relative ammonium contribution to N uptake decreases by a few percent.

Converting nitrate into ammonium does not affect the total-N concentration in the soil solution if K_a = 0 cm^3 cm^{-3}, and leads to a lower total-N concentration if

Table 2. Calculated N uptake and NH_4-N uptake (kg ha^{-1}) during the growing season, as affected by a 20% reduction in N demand (NDEM), transpiration rate (TRANSP) or root length density (LRV).

Treatment	N uptake	NH_4-N uptake	NH_4-N uptake/ N uptake
Standard input	61.0	16.6	0.27
NDEM	53.7	16.1	0.30
NDEM, TRANSP	51.4	15.7	0.31
LRV	57.7	13.6	0.24
LRV, TRANSP	55.0	13.2	0.24
LRV, TRANSP, NDEM	48.2	12.8	0.27

$K_a = 2\ cm^3\ cm^{-3}$. In neither of the two situations is total-N uptake affected to any extent. Ammonium uptake, on the other hand, strongly increases for both K_a values, compared with the standard situation. If $K_a = 0\ cm^3\ cm^{-3}$, even more than half of the N taken up consists of ammonium.

Effect of reduced N demand, transpiration rate or root density

Many forests in areas with high NH_x input are in poor condition, so the growth rate of the trees may decrease, which may result in a reduced N demand, a lower transpiration rate (thus water extraction rate) and a smaller root growth rate and/or higher root turn-over rate, thus a smaller root length density. The effect on calculated N uptake of a 20 % reduction in the value of these parameters is shown in Table 2.

A smaller N demand leads to a smaller N uptake, while the ammonium uptake changes little; the ammonium contribution to N uptake thus slightly increases (from 27 to 30 %). If not only N demand decreases but also the transpiration rate, then both N uptake and ammonium uptake decrease; the ammonium contribution is unaffected, compared to the situation with only a reduced N demand.

A reduction in root length density has a negative effect on ammonium uptake; the relative ammonium contribution to N uptake decreases from 27 to 24 %. If water availability is a limiting factor (as in this forest site), a reduction in root length will be accompanied by a reduction in total water extraction rate of the roots, and thus by reduced transpiration rate. Since N uptake as well as ammonium uptake then slightly decrease, the relative ammonium contribution to N uptake is not further reduced.

If N demand as well as transpiration rate and root length density decrease, the total-N uptake strongly decreases, but the relative ammonium contribution to N uptake is not affected, compared to the standard situation.

Discussion

All calculations were carried out using results of measurements at the acidification research site at Kootwijk in 1988. At other locations or in years with different weather conditions, parameter values – and thus results – may differ considerably from the ones presented here. Moreover, the model could not be validated, since detailed measurements on N source taken up were not carried out and (probably) are impossible under field conditions. Interpretation of the results, therefore, should not be focussed on small differences in calculated values of this specific forest site, but on main effects and general trends.

Total-N uptake rate

The total-N uptake rate can only meet the N demand during early spring and from late summer onwards, but during a large part of the growing season the uptake is not nearly fast enough to fulfil the N demand. In addition to N uptake by the roots, the trees may also meet part of their N demand by taking up atmospheric NH_x and NO_x, either in gaseous form or after deposition on the leaves (see e.g. van Hove et al., 1987; 1989). For this forest stand the annual atmospheric N uptake was estimated to be about 5.1 kg ha^{-1} (Mohren, pers. comm.).

From the measured biomass increase and N concentrations, the actual N uptake of the forest was calculated by Mohren and colleagues (pers. comm.). They arrived at a value of 80 kg ha^{-1} yr^{-1}, which, after subtracting atmospheric N uptake, leaves about 75 kg ha^{-1} yr^{-1} taken up by the roots. We calculated an N uptake value between 61 and 79 kg ha^{-1} yr^{-1}, depending on the input data used (average or maximum values), hence in the same range. Higher calculated N uptake should be possible in case that the possibility of (extreme) synlocation of roots and high-N-input sites (dripping zones) should be included in the model. Data for such calculations, however, are not available.

Comparing the two model approaches

Calculated total-N uptake is the same with both model approaches, but the fraction of N taken up as ammonium (Figure 5) and the contribution of roots in various layers to N uptake (Figures 6 and 7) are different. Interaction between uptake of ammonium and nitrate is well known from nutrient solution experiments (e.g. MacKnown et al., 1982; Breteler & Siegerist, 1984; Criddle et al., 1988). In these experiments a mixture of the two N sources was supplied to whole root systems, while in the field situation considered here, different root zones were supplied with different ammonium/nitrate ratios at different total-N levels. Effects of local N supply to part of the root system were reported by Drew & Saker (1975) and de Jager & Schrier (1985). However, they used only a single N source. To determine which of the two model approaches presented here is more realistic, results are needed from split-root experiments in which ammonium is supplied to one part of the root system and nitrate or ammonium nitrate to another. This information is not available as yet.

It is, therefore, impossible to judge the accuracy of either model approach; reality probably will be somewhere in between. The relative ammonium contribution to N uptake on whole-tree level, however, will not exceed the value calculated by the 'approach with priority to ammonium uptake', the more since ammonium preference probably is not as absolute as in the present calculations (Keltjens & van Loenen, 1989; Gijsman, 1991; Kamminga-van Wijk, in prep.). The ammonium contribution to N uptake within individual soil layers, however, may be highest with the 'approach with priority to uniform N uptake' (Figure 7).

Contribution of ammonium to N uptake and its consequences

Considering the effects of N source taken up on tree growth and functioning, a distinction should be made between the ammonium contribution to N uptake by the tree as a whole and the ammonium contribution to N uptake by roots within a certain layer. From ionic balance experiments with Douglas-fir on acid soil, Gijsman & van Noordwijk (1990) calculated that when more than about 80 % of the N taken up on whole-tree level consists of ammonium, physiological disorders may be expected. Under the present conditions, such disorders are not likely to happen, since high relative ammonium contributions only occur temporarily. Furthermore, the tree will be able to bridge short periods with high ammonium uptake via its carboxylate reserves, since the physiological disorders are related to redistribution of carboxylates between shoot and roots (see e.g. Raven & Smith, 1976; Davies, 1986).

Proton excretion probably is a response of a more local character (cf. Römheld, 1986; Römheld & Marschner, 1986), since ammonium has to be metabolized soon after absorption, thus leading to a local proton production. On the basis of the present calculations, rhizosphere acidification may be expected in the top soil, since roots in these layers take up a large part of their N in ammonium form. Due to the high organic matter content in the forest top soil, the reduction in rhizosphere pH may yet be only a few tenths of a unit, as indeed was found in this forest (Gijsman, unpublished data).

Long-term effects

A reduction in N demand during the period of unconstrained uptake will lead to an equivalent reduction in N uptake rate during that period. On the other hand, a reduction in N demand during the period of constrained uptake will not necessarily result in reduced N uptake rate: cumulative N demand in this period was about 70 kg ha^{-1}, while calculated cumulative N uptake was only about 25 kg ha^{-1}. This implies that even a very large reduction in N demand would not affect N uptake in the period of constrained uptake. Since the ratio of N uptake rate and N demand varies with time, no exact value can be given for the degree of such a reduction in N demand that does not affect N uptake.

From Figure 5 it appears that during almost the entire first period of unconstrained uptake (22 March – 2 May), ammonium uptake greatly exceeds nitrate uptake; in the second period (16 July – 15 November) this is only true for a short interval. Hence, a reduction in N demand – and thus in total-N uptake – may lead to a strong increase in the relative ammonium contribution during this second period. However, the effect on the relative ammonium contribution, integrated over the whole season, will be small (cf. Table 2).

To explain soil acidification due to NH_x deposition, van Diest (1989) presented a theory of a reduced rate of ammonification of soil organic matter, leading to incomplete neutralization of protons excreted during nutrient uptake. A central assumption in his theory is that the trees take up most of their N in the ammonium form. The results of the calculations presented here do not support this hypothesis for the ACIFORN site at Kootwijk, even though calculations were based on absolute ammonium preference. Even a 20 % increase in ammonium concentration does not lead to a significantly higher ammonium contribution to N uptake (Table 1). If, however, nitrate availability is reduced while at the same time ammonium availability is increased (Table 1), the relative ammonium contribution to N uptake may increase dramatically, depending on the ammonium adsorption coefficient. With increasing soil acidification, it may be expected that a larger fraction of the soil cation exchange complex will be occupied by H^+ and Al^{3+} ions, so K_a will decrease. A reduction in nitrification rate will then result in an increased ammonium contribution to N uptake.

At present, the situation of a strongly dominant ammonium uptake has not yet been reached in this forest. If, however, the NH_4^+/NO_3^- ratio in the soil solution should drastically increase – e.g. due to reduced nitrification rate – this situation could be reached.

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