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Measured and modelled differences in nutrient concentrations between rhizosphere and bulk soil in a Norway spruce stand

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Abstract

The gradient in soil characteristics from the bulk soil to the root surface is important to roots and to the organisms that live in the rhizosphere. Our ability to measure ion concentrations at the root surface is extremely limited, and models are largely untested. We used data from a well studied Norway spruce stand in SW Sweden to compare the measured difference in nutrient concentrations between rhizosphere and bulk soil with the difference predicted by a steady-state simulation model based on ecosystem budgets of nutrient uptake. The simulation model predicted depletion of NH_4, Ca, Mg, K in the rhizosphere, which shows that budgeted uptake rates were greater than the mass flow of bulk solution towards the root. In plots treated with ammonium sulphate, the model predicted an accumulation of S in the rhizosphere. In contrast, the observed rhizosphere concentrations were generally enriched in nutrients, relative to bulk soil. Collecting rhizosphere soil adhering to root surfaces may not be an appropriate method for describing the concentration gradient around the root. In addition, the simulation model omits some processes affecting conditions in the rhizosphere that are important to explaining nutrient uptake.

Introduction

The soil near root surfaces can differ dramatically from bulk soil. Measured differences between rhizosphere and bulk soil nutrient concentrations have been attributed to a variety of factors. Some factors are specific to the rhizosphere, such as reduced pH (Dieffenback and Matzner, 2000; Wang et al., 2001), complexation of metals by root exudates (Mench et al., 1992), enhancement of mineral weathering (Leyval and Berthelin, 1991) and acceleration of decomposition. Another important factor is whether the rate of nutrient uptake exceeds the rate of nutrient supply to the root surface via mass flow, which is the movement of soil solution to the root driven by transpiration. Opportunities to test the validity of this last explanation are rare, because of the number of measurements required to calculate nutrient uptake, nutrient supply in mass flow, and thereby the concentration gradient attributable to root uptake.

Nutrient uptake models simulate the concentration of nutrients in soil and soil solution as a function of distance from the root surface (Barber, 1984; Nye and Tinker, 1977; Yanai, 1994). For limiting nutrients, rhizosphere soil is predicted to have lower concentrations than the bulk soil, because the capacity of the root to take up nutrients exceeds their rate of movement through the soil by mass flow and diffusion. In contrast, ions that are excluded from the root, such as aluminum, are predicted to have higher concentrations in the rhizosphere than in bulk soil.

There are several approaches to measuring differences between rhizosphere and bulk soil. The most common method is to collect rhizosphere soil adhering to roots, followed by extraction (Bakker et al., 1999; Gobran and Clegg, 1996) or centrifugation (Wang

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and Zabowski, 1998). Alternatives include microelectrodes (Dieffenbach and Matzner, 2000), microsuction cups (Wang et al., 2001), and thin-sectioning from a rhizotron (Gollany et al., 1997; Smith and Pooley, 1989). Indirect methods include comparing soil with and without plants (Leyval and Berthelin, 1991), but these do not provide an estimate of the concentration gradient around the root.

The purpose of this study was to compare empirical measurements with theoretical predictions of the differences between rhizosphere and bulk soil chemistry at a single well-studied site. The site was a Norway spruce stand in southwest Sweden at which rhizosphere and bulk soil was collected for 3 years from control plots and plots treated with ammonium sulphate (Majdi and Persson, 1995). Although the response of rhizosphere and bulk soil to treatments has been reported (Majdi and Rosengren-Brink, 1994), the chemistry of the two soil fractions has not previously been compared. In addition to this empirical characterization of the accumulation or depletion of ions near root surfaces, we applied a nutrient uptake model (Yanai, 1994) to describe the theoretical concentration gradient consistent with estimated rates of nutrient uptake, root length density, transpiration rates, and soil properties. We expected to find that both measured and modelled comparisons of bulk and rhizosphere soil would show major nutrient elements to be depleted near root surfaces, while solutes less in demand, such as Na, would show accumulation. The treatment provided elevated ammonium and sulphate concentrations, more likely to produce accumulation of nitrogen and sulphur at the root surface.

Because nutrient uptake rates had not previously been estimated at this site, a supporting objective of this study was to calculate ecosystem budgets for the major nutrient elements. Uptake at the ecosystem scale was budgeted as the sum of nutrient fluxes in litterfall, foliar leaching, and fine root turnover, plus nutrient accumulation in above- and belowground biomass. The uptake rate was used to simulate the concentration gradient around the roots, and thus the difference between bulk and rhizosphere soil concentrations.

Materials and methods

Site description

The study site is a second-rotation Norway spruce stand planted in 1966 in southwest Sweden (56° 33′ N, 13° 13′ E), 95–115 m above sea level. The soil at the site is a stony sandy loam Haplic podzol developed in glacial till. The $pH_{(H_2O)}$ prior to treatments was 3.9 in the Oa horizon and 4.1 in the upper mineral soil. The effective base saturation was 30% in the Oa and varied from 7 to 12% in the mineral soil. Further physical and chemical characteristics of the soil are described by Bergholm et al. (1995).

Field plots measuring 45 × 45 m were established in 1987 in a randomised experimental design with four blocks and six treatments (Bergholm et al., 1995). Treatments were started in 1988; roots and soil were sampled in 1989, 1990 and 1992 from control plots and from those treated with annual additions of 100 kg NH_4-N ha^{-1} and 114 kg SO_4-S ha^{-1} (Majdi and Bergholm, 1995; Majdi and Rosengren-Brink, 1994).

Bulk and rhizosphere soil sampling

Ten cylindrical cores 4.5 cm in diameter were taken in each plot (40 for each treatment) during the last week of September in 1989, 1990 and 1992. Soil cores were collected from the mineral soil at depths of 0–10, 10–20 and 20–30 cm and subsampled in the field. The samples were stored in a freezer at −18 °C and moved to a refrigerator at 4 °C for 4 h before processing. Root fragments with attached soil were carefully picked out by hand. Bulk soil was separated from rhizosphere soil by shaking the excavated root fragments very gently in a plastic container: soil that did not adhere to the roots was considered to be bulk soil. Rhizosphere soil was the 0–2-mm thick layer of the soil attached to the fine roots, which was removed from the root by brushing. The soil samples were equilibrated at a soil:water ratio of 1:2 by weight (Majdi and Bergholm, 1995) at 20 ± 1 °C for 24 h with continuous shaking. They were then centrifuged at 9000 × *g* for 10 min, whereupon the supernatant solution was removed, passed through a 0.45-μm millipore filter, and analysed for pH. Inductively coupled plasma spectroscopy was used to analyse Ca, Mg, K, and Na in the soil water extract; NH_4 and NO_3 were analyzed by flow injection analysis, and SO_4 was measured by ion chromatography. Ammonium was measured only in 1992. We used analysis of variance with ammonium sulphate treatment, soil layer, and sampling time as the main factors to determine differences in elemental concentrations between bulk and rhizosphere soil.

Modeling approach

Most of the parameters required by the simulation model were available from the study site. Root uptake capacity (α, described below) was not measured at this site, but was assumed to have the value required to explain the budgeted rate of nutrient uptake by the stand. This value was used in the simulation model to predict the degree of accumulation or depletion of ions in the rhizosphere compared to bulk soil. This prediction by the model could then be compared to the empirical measurements of bulk and rhizosphere soil in the same experimental system.

The O horizon was not included in the comparison of bulk and rhizosphere soil because it is too difficult to remove organic material from roots. This horizon contains 50% of fine roots (Majdi, 2001) and is presumably important to nutrient uptake. For modelling purposes, we assumed that half of the nutrients required to explain the budgeted uptake rates were taken up from the mineral soil horizons, but this proportion is quite uncertain. It is also unknown how nutrient uptake rates vary seasonally. We assumed that roots are active for 6 months of the year at the study site (May–October). The result of assuming that uptake occurs over twice as many roots as we simulated during half of the year is the same as assuming that all of the uptake occurs from the modelled mineral soil horizons and that roots are active year round. We tested the importance of these assumptions by alternately assuming that uptake occurs from only the modelled mineral soil horizons and for only half the year (i.e., uptake rates are double that of our first guess).

Model description

We used a steady-state model (Baldwin et al., 1973; Yanai, 1994) to simulate the concentration gradient between the root surface and bulk soil, using parameters that describe soil chemistry, root morphology, and nutrient uptake kinetics. The model represents solute movement through the soil by diffusion and mass flow, and uptake at the root surface by a concentration-dependent function.

The concentration of a solute at the root surface (C_0, μmol L^{-1}) can be described as a function of the average concentration in solution:

$$C_0 = C_{\mathrm{av}} v_0 \left[\alpha + (v_0 - \alpha) \left(\frac{2}{2-\gamma} \right) \frac{r_x/r_0)^{2-\gamma} - 1}{r_x/r_0)^2 - 1} \right]^{-1},$$

where C_{av} is the average solution concentration (μmol L^{-1}), α is the root absorbing power (mm s^{-1}), v_0 is the inward radial velocity of water at the root (mm s^{-1}), r_x is the average radial distance to the next root's zone of influence (mm), r_0 is the radius of the root (mm), and γ is $r_0\, v_0/(Db)$ (dimensionless), where D_e is the effective diffusion coefficient (mm^2 s^{-1}) and b is the buffer capacity of the soil, or the ratio between exchangeable and dissolved nutrient (dimensionless).

Model parameters

The parameters in the model that describe rooting geometry are radius and root length density, represented by the half-distance to the next root (Table 1). We used an average root diameter of 0.5 mm, as more than 85% of spruce roots at the study site have diameters between 0.2 and 1 mm (Majdi and Rosengren, 1994). Root length was calculated using the measured mass and specific root length. The half-distance to the next root is a measure of root length density, which was calculated from root length.

To estimate root length, 10 cylindrical soil samples were taken from each plot in three mineral soil layers, 0–10, 10–20 and 20–30 cm, in 1989, 1990, and 1992. Fine roots <2 mm in diameter were separated from the soil by hand. Living roots were identified on the basis of colour, structure of the cortex or bark, and colour of the stele. The living roots are more resilient and firm and have good adhesion between the cortex and periderm. Root length was measured using a Comair root length scanner.

Soil parameters include the bulk soil solution concentration, the effective diffusion coefficient, and the rate of water movement towards the root. Bulk soil solution concentrations were measured in water extracts of soil, as described above. The effective diffusion coefficient (D_e) of the solute through the soil for each nutrient was calculated as $D_l \cdot \theta \cdot f/b$ (van Rees et al., 1990), where D_l is the diffusion coefficient in water, obtained from the conductivity of each solute (Lide, 2000), θ is the volumetric water content, and f is the fugacity, calcuated as $3.13\theta^{1.92}$ (van Rees et al., 1990). Soil water content was simulated using the SOIL Model (Jansson and Halldin, 1979).

We did not estimate b, the buffer capacity, because the effective diffusion coefficient appears in the model multiplied by b, and the result is insensitive to the value of b. Finally, the radial velocity of water uptake at the root surface was calculated as $2\pi \times r_0 \times L/T$, where $2\pi \times r_0 \times L$ is the root surface area, and T

Table 1. Parameters used in the uptake model in control and ammonium sulfate (NS)-treated plots. A range of values is shown for the average half-distance to the next root (r_x) and the inward radial velocity of water at the root surface (v_0) because they are calculated for each horizon, treatment, and year; the average solution concentration (C_{av}) and the effective diffusion coefficient (D_e) further depend on the nutrient simulated. The root absorbing power (α) was assumed constant across horizons and years. The root radius (r_0) was assumed constant for all conditions

Nutrient	Treatment	Parameter					
		r_x (mm)	r_o (mm)	v_o (nm s^{-1})	α (nm s^{-1})	C_{av} (μmol L^{-1})	D_e (μm^2 s^{-1})
NH_4	Control	3.6–4.4	0.5	1.8	9.5	52–215	6.4–15
	NS	3.5–4.6	0.5	1.8	4.7	291–642	8.4–17
S	Control	3.6–5.5	0.5	1.6–2.1	3.2	28–51	2.6–9.0
	NS	3.4–5.3	0.5	1.6–1.8	1.3	77–295	2.6–9.0
Ca	Control	3.6–5.5	0.5	1.6–2.1	41.1	4–9	1.9–6.7
	NS	3.4–5.3	0.5	1.6–1.8	7.7	14–51	1.9–6.7
Mg	Control	3.6–5.5	0.5	1.6–2.1	1.9	18–47	1.7–6.0
	NS	3.4–5.3	0.5	1.6–1.8	2.1	30–100	1.7–6.0
K	Control	3.6–5.5	0.5	1.6–2.1	1.5	28–142	4.8–17
	NS	3.4–5.3	0.5	1.6–1.8	1.7	30–202	4.8–17

is the transpiration rate, which was simulated using the SOIL model (Jansson and Halldin, 1979). We distributed transpiration over the soil layers by assuming that water uptake was proportional to the root length or surface area.

We did not measure nutrient uptake kinetics. There are measurements of relative uptake capacity of PO_4 and SO_4 on excised roots of the Norway spruce from our study site (Clemensson and Asp, 1995), but these were not made at concentrations representative of the soil solution. We calculated the annual rate of nutrient uptake by ecosystem budgets (as described below), and then used this rate to determine the uptake kinetics at the root surface (represented by α) necessary to produce this rate of uptake from the observed solution concentrations in the bulk soil. We assumed that N was taken up as NH_4, because NO_3 concentrations in the soil water were negligible (Bergholm and Majdi, 2001) and because spruce roots preferentially take up NH_4 (Chalot et al., 1995).

Budgeted nutrient uptake

An ecosystem budget estimates the rate of nutrient uptake required to account for the observed sinks for the nutrient. Nutrient uptake is thus the sum of litterfall, foliar leaching, root turnover, and aboveground and belowground biomass accumulation.

Litterfall was measured using circular litter traps in 1989, 1990 and 1992 (Nilsson and Wiklund, 1992). Foliar leaching was measured in 1989, 1990, 1992 and 1993 using 15 polyethylene funnels 20 cm in diameter in each plot (Bergkvist and Folkeson, 1995). The turnover rate of nutrients in fine roots was estimated as the nutrient content divided by the median lifespan of roots obtained by minirhizotrons. The median lifespan of fine roots for control and ammonium-sulphate treated plots during 1991–1993 was 0.9 and 0.8 years, respectively (Majdi and Kangas, 1997). The amount of fine roots in 1989, 1990 and 1992 was measured as described above. The dried roots were milled and wet-digested with concentrated nitric and perchloric acids heated to 150 °C. Calcium, Mg, P, K and S were analysed by inductively coupled plasma emission spectroscopy (ICP). An elemental analyser (Carlo Eerba NA 1500) measured N and carbon.

The accumulation of nutrients in aboveground stem wood, stem bark, living and dead branches and needles was estimated by destructive sampling as the difference between nutrient amount in 1990 and in 1987 (Nilsson and Wiklund, 1995). To calculate the annual increment in coarse root biomass, we used a regression equation based on tree diameter and height in each year (Nihlgård, 1972). Fine root accumulation was negligible (the amounts of nutrients in fine roots did not change significantly from year to year) (Bergholm and Majdi, pers. comm.).

We also report some other pool sizes and flux rates to provide context. Aboveground biomass was the initial biomass in control and treated plots in 1987. Fine root biomass was the average from soil cores collected in 1989, 1990 and 1992 (Majdi and Persson, 1995). Coarse root biomass was calculated for 1987 using a regression equation (Bergholm and Majdi, pers. comm.). Wet deposition and throughfall were sampled during two periods, 1989–1990 and 1993–1994 (Bergholm and Majdi, 2001). The dry deposition of elements was estimated using the ratio of Cl in throughfall and wet deposition.

Results

Observed rhizosphere and bulk soil concentrations

Concentrations of elements in both rhizosphere and bulk soil generally declined with soil depth and were higher in the ammonium-sulphate treated plots (Figure 1). Concentrations also tended to decline over time: for K, Mg, and Na, the declines were statistically significant in two of the three intervals defined by our sampling dates (89–90, 89–92, 90–92). Sulphate increased for 89–90 but decreased from 90–92. Other contrasts and elements were not statistically significant.

The observed differences between rhizosphere and bulk soil concentrations were quite variable (Figure 1). There was a universal accumulation of K in the rhizosphere for all years and soil horizons. Calcium, Mg and Na also showed statistically significant accumulation in the rhizosphere. There was no consistent pattern of accumulation or depletion for S or NO_3.

Budgets

Nutrient budgets showed uptake of the major nutrient elements in about the expected proportions, in the order N, Ca, K, S, Mg, P (Figure 2). The relative importance of the various sinks for nutrients varied according to the element. Throughfall was an important flux for S and K, which are mobile ions. Litter production was most important for Ca, followed by N, P, and Mg. Fine root turnover was most important for P and N budgets. Uptake of all elements was stimulated by ammonium sulphate additions, in part because growth was stimulated (biomass was 15% greater in treated plots by 1990 and 23% by 1993) (Bergholm and Majdi, pers. comm.). The greatest increases were observed in N and S uptake (79 and 75%, respectively). Uptake of Ca, Mg, and K, which were not applied in the ammonium-sulphate treatment, increased by about 40%. Foliar leaching showed a large increase in K and S in the ammonium-sulphate treatment.

Biomass pools (Table 2), like fluxes, were greater in the ammonium-sulphate treated plots. Fertilizer additions were large compared to background rates of atmospheric deposition of N and S. Much of the added N was retained in biomass (43%), but not much of the S (4%).

Simlulated rhizo-bulk differences

The budgeted rates of uptake (Figure 2) were used in conjunction with the other parameters in the nutrient uptake model (Table 1) to find α, the root absorbing power, for each element. Using these estimates of α (Table 1) and the concentrations measured in bulk solution, we predicted the solution concentrations at the root surface (Equation (1)).

The model predicted depletion in the rhizosphere for NH_4 and Ca, compared to bulk soil, in every horizon and year in both control and ammonium-sulphate treated plots (Figure 3). Model predictions for Mg depended on the year and treatment, but were generally higher in the rhizosphere than the bulk soil. Simulated accumulations in the rhizosphere mean that the observed (budgeted) uptake of nutrients were greater than would be supplied by the transpiration stream given the reported bulk soil solution concentrations. In contrast, the model predicted accumulation of K in the rhizosphere in most years in both treatments, indicating that the K concentration in the bulk solution was greater than that required to explain the observed uptake, and the calculated root absorbing power was therefore less than the rate of delivery of K to the root surface by bulk flow. For S, the model predicted depletion in the control, but accumulation in the treatment. This means that the increased concentrations of S in solution in the treated plots were greater than necessary to explain the observed increase in S uptake; active uptake was required to explain the observed sinks for S in the control plots, while exclusion was required in the treated plots.

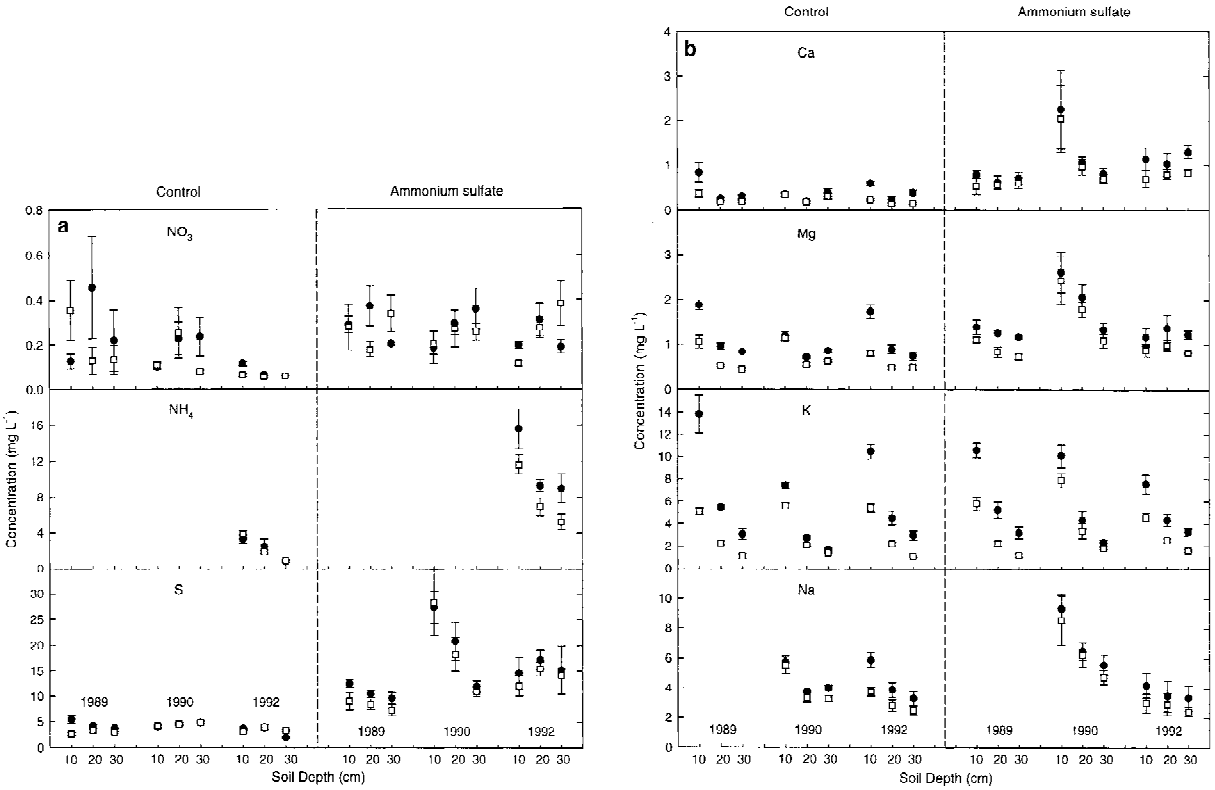

Figure 1. Bulk (□) and rhizosphere (●) nutrient concentrations measured by soil extraction. (a) NO_3, NH_4, and S. (b) Ca, Mg, K, and Na. Error bars show the standard error of the mean.

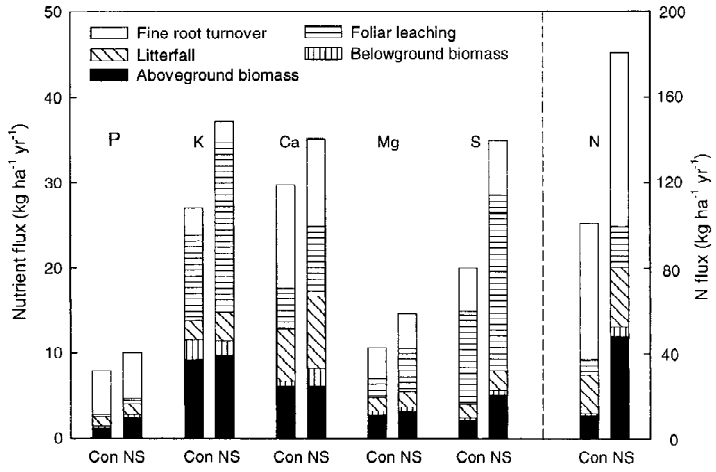

Figure 2. Nutrient fluxes for a Norway spruce stand in control (C) and ammonium sulfate (NS)-treated plots. Uptake is the sum of nutrient fluxes in above- and below-ground biomass accumulation, litterfall, foliar leaching, and fine root turnover.

Table 2. Nutrient pools and inputs for a Norway spruce stand in control and ammonium sulfate (NS)-treated plots, measured between 1987 and 1992

Components	N	P	K	Ca	Mg	S
Control						
Pool sizes			kg ha^{-1}			
Aboveground biomass	315	31.1	134.9	163	33.8	31.8
Belowground biomass						
Fine roots	48	3.8	2.5	9.3	2.8	3.8
Coarse roots	31	3.0	14.8	21.6	4	3
Total	395	37.9	152.2	193.9	40.6	38.6
Input			kg ha^{-1}	year^{-1}		
Wet and dry deposition	22	0.4	4.6	5.1	5	24.2
NS						
Pool sizes			kg ha^{-1}			
Aboveground biomass	346	34.2	148.4	179.3	37.2	35
Belowground biomass						
Fine roots	57	3.7	1.7	7.1	1.7	4.4
Coarse roots	35	3.4	16.8	24.5	4.5	3.3
Total	438	41.3	166.9	210.9	43.4	42.7
Input			kg ha^{-1}	year^{-1}		
Wet and dry deposition	22	0.4	4.6	5.1	5	26
NS addition	100	0	0	0	0	114
Total	122	0.4	4.6	5.1	5	140

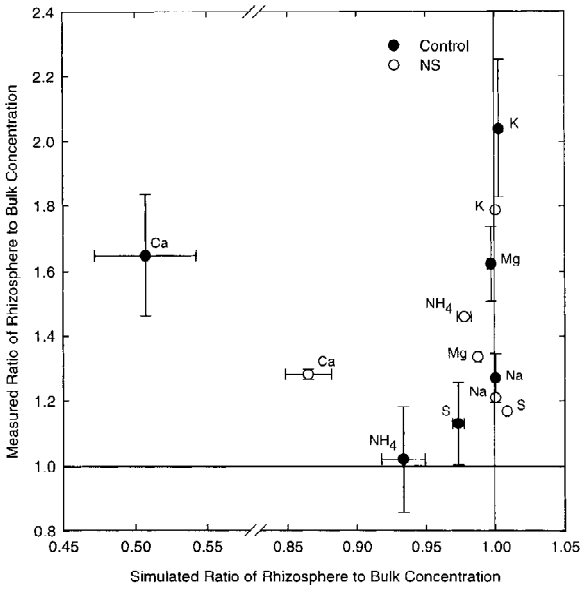

Figure 3. Comparison of simulated and measured differences between rhizosphere and bulk soil. Error bars show the standard error of the mean of 3 years and three horizons in each year, except for NH_4, which was measured in only 1 year. Rhizosphere Na could not be simulated for lack of budgetary information, and the simulated ratio is therefore arbitrarily graphed at 1.0.

Comparison of observed and simulated rhizo-bulk differences

In general, the model predicted depletion of nutrients near the root surface, but the measurements indicated accumulation (Figure 3). Only for K was there agreement between the observed and simulated comparison of rhizosphere and bulk soil concentrations, with both indicating accumulation.

Another striking disagreement between the simulated and observed ratios of rhizosphere and bulk soil concentrations, regardless of whether depletion or accumulation is at issue, is the magnitude of the difference. The model simulated differences of 4% between bulk and rhizosphere concentrations for NH_4, and less than 1% for S, Mg and K (Figure 3). For Ca, the model predicted depletions that were conceivably measurable, averaging 14% in the ammonium-sulphate treated plots and 49% in the controls. The observed rhizosphere concentrations, in contrast, could exceed those in bulk soil by a factor of two or more, for Ca, Mg, K and S.

Sensitivity analysis

The effect of doubling the assumed rate of nutrient uptake was always to reduce simulated rhizosphere concentrations, but this effect was small in most cases. Doubling the rate of S, NH_4, Mg, and K resulted in reductions in simulated rhizosphere concentrations of 4, 5, 1 and 2%, respectively, averaging over horizons, years, and treatments. In contrast, doubling the rate of budgeted Ca uptake input to the simulation model resulted in dramatic changes to the simulated rhizosphere depletion. In ammonium-sulphate-treated plots, the rhizosphere concentration was reduced by an average of 29%, and in control plots, concentrations were reduced by 85%. The greater sensitivity of Ca and especially of Ca in untreated plots is due to the low concentration of Ca in solution (Table 1) relative to the observed uptake (Figure 2), which results in high values of the root absorbing power, α (Table 1), and the most severe simulated depletion, as described above.

Discussion

The differences between rhizosphere and bulk soil nutrients measured by soil extractions did not agree with the differences in solution concentration simulated by the model. There are a variety of methods for characterizing rhizosphere conditions; the one we used (mechanical removal of soil adhering to the roots followed by extraction) may not be the most suitable for describing the soil solution. Other studies using this method (Bakker et al., 1999; Wang and Zobowski, 1998; Phillips and Yanai, pers. comm.) had similar results to ours, with rhizosphere concentrations of nutrients generally greater than those of bulk soil. In contrast, studies using microlysimeters have reported depletion of nutrients in the rhizosphere (Gottlein et al., 1999; Wang et al., 2001) (but not in the case of Dieffenback and Matzner, 2000). Soil removed from the root includes root exudates and sloughed root cells, which are important to explaining processes in the rhizosphere, but are not included in a model of solute uptake and movement by diffusion and mass flow. The micro-lysimeter methods may be more suitable to testing these models.

Just as different methods of measuring rhizosphere soil produce different results, different models could produce different estimates of rhizosphere concentrations. There are two main sources of error to consider in assessing the reliability of model simulations. First, the model formulation may be erroneous, if it does not correctly include the factors most important to the process being simulated. In the case of nutrient uptake, models such as the one we used would incorrectly predict nutrient concentrations at the root surface if sources of nutrients in the rhizosphere are important to uptake, because these are not included in the model. Both the mineralization of organic matter and the weathering of minerals (Leyval and Berthelin, 1991) may be accelerated by the action of roots and microbes in the rhizosphere. Norway spruce can take up nitrogen in organic form (Öhlund and Näsholm, 2001); uptake of nutrients in organic form was not included in our model. Another factor not included in the model is the role of extramatrical mycorrhizal hyphae in nutrient uptake. For example, in citrus seedlings, mycorrhizae can increase P uptake beyond that predicted by the model, even when the uptake capacity of the mycorrhizal roots is taken into account (Eissenstat and Yanai, 1997). The approach we used did not rely on measurements of nutrient uptake capacity of roots, but the model assumes that nutrients are taken up at the root surface from the soil solution. If hyphal uptake occurs at a distance from the root, nutrient concentrations at the root surface would tend to be underestimated by the model.

The second source of error in simulation modeling is inaccurate determination of parameter values. One way to assess the effect of uncertainty in the parameter values is to conduct a sensitivity analysis, which examines the effect of changing parameter values on the simulation results. Previous investigations of the model we used (Equation (1)) showed that the bulk solution concentration (C_{av}) and the nutrient uptake capacity (α) were likely to be the most important factors controlling uptake per unit root length, and that interactions of parameters were important, such that the sensitivity of the model to one parameter depended on the values of other parameters (Williams and Yanai, 1996; Yanai, 1994).

In the current investigation, the parameters and model outputs were rearranged: instead of simulating uptake, rates of uptake estimated from ecosystem budgets (Figure 2) were used as model input, and nutrient uptake capacity was simulated, not measured. The output of the model was the concentration at the root surface, or the amount of accumulation or depletion of the soil solution in the rhizosphere compared to the average in bulk soil. In this formulation, whether accumulation or depletion is simulated depends on

whether bulk flow of nutrients in the soil solution (the transpiration rate (v_0) times the concentration in the bulk solution (C_{av})) exceeds the reported uptake rate.

The least certain of the estimates in this calculation was probably the reported uptake rate, which depends on budgets summing above- and below-ground biomass accumulation, litterfall, foliar leaching, and fine root turnover (Figure 1). This annual uptake rate was converted to uptake at the root surface using additional assumptions regarding the length of the active uptake season and the distribution of uptake over soil horizons, which are also highly uncertain. Fortunately, our sensitivity analysis, in which uptake rates were doubled, showed little effect on the simulation of rhizosphere concentrations, except in the case of Ca, and no effect on predicted depletion versus accumulation (whether rhizosphere concentrations were greater or less than bulk soil concentrations). Thus the test of whether observed rhizosphere accumulation or depletion was explained by the rate of nutrient delivery to the root exceeding or not exceeding the rate of nutrient uptake was robust to variation in the assumed uptake rate. But the test failed: the observed comparisons of rhizosphere and bulk soil concentrations did not correspond with the simulated ones. Different methods of observing the rhizosphere might be more appropriate to characterizing the concentration gradients around roots, as discussed above. When such methods become available, they will be valuable to improving the formulation of models of nutrient uptake.

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