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REGULAR ARTICLE

The vertical distribution of N and K uptake in relation to root distribution and root uptake capacity in mature *Quercus robur*, *Fagus sylvatica* and *Picea abies* stands

Hans Göransson · Morten Ingerslev · Håkan Wallander

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Abstract We have measured the uptake capacity of nitrogen (N) and potassium (K) from different soil depths by injecting ^{15}N and caesium (Cs; as an analogue to K) at 5 and 50 cm soil depth and analysing the recovery of these markers in foliage and buds. The study was performed in monocultures of 40-year-old pedunculate oak (*Quercus robur*), European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies* (L.) Karst.) located at an experimental site in Palsgård, Denmark. The markers were injected as a solution through plastic tubes around 20 trees of each species at either 5 or 50 cm soil depth in June 2003. After 65 days foliage and buds were harvested and the concentrations of ^{15}N and Cs analysed. The recovery of ^{15}N in the foliage and buds tended to be higher from 5 than 50 cm soil depth in oak whereas they where similar in spruce and beech after compensation for differences in immobilization of ^{15}N in the soil. In oak more Cs was recovered from 5 than from 50 cm soil depth whereas in beech and spruce no difference could be detected. Out of the three investigated tree species, oak was found to have the lowest capacity to take up Cs at 50 cm soil depth compared to 5 cm soil depth also after compensating for differences in discrimination against Cs by the roots. The uptake capacity from 50 cm soil depth compared with 5 cm was higher than expected from the root distribution except for K in oak, which can probably be explained by a considerable overlap of the uptake zones around the roots and mycorrhizal hyphae in the topsoil. The study also shows that fine roots at different soil depths with different physiological properties can influence the nutrient uptake of trees. Estimates of fine root distribution alone may thus not reflect the nutrient uptake capacity of trees with sufficient accuracy. Our study shows that deep-rooted trees such as oak may have lower nutrient uptake capacity at deeper soil layers than more shallow-rooted trees such as spruce, as we found no evidence that deep-rooted trees obtained proportionally more nutrients from deeper soil layers. This has implications for models of nutrient cycling in forest ecosystems that use the distribution of roots as the sole criterion for predicting uptake of nutrients from different soil depths.

Keywords Cs · ^{15}N · Nutrient uptake · Tree root distribution · Oak · Beech · Spruce

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H. Göransson (✉)
Institute of Integrative Biology,
ETH, Universitätstrasse 16,
CHN 8092 Zürich, Switzerland
e-mail: hans.goeransson@env.ethz.ch

M. Ingerslev
Danish Forest Landscape Research institute,
Hoersholm Kongevej 11,
2970 Hoersholm, Denmark

H. Wallander
Department of Microbial Ecology, Lund University,
Ecology Building,
SE-223 64 Lund, Sweden

Introduction

The base saturation in forest soils of southern Sweden has declined during recent decades, mainly due to the removal of nutrients during harvesting and by leaching and loss of nutrients below the root zone (Jönsson et al. 2003). This indicates that the addition of base cations by deposition and weathering is slower than the depletion, which means that the forest ecosystem is not sustainable with regard to base cations. If this decrease continues there would be a shortage of base cations, which may lead to nutrient imbalance in the trees. A nutrient imbalance may affect the growth and the capacity of the trees to resist stress, for example frost and pathogens (Jönsson 2000a, b; Katzensteiner et al. 1992; Thelin 2000). Nutrient uptake occurs mainly through the fine roots and their associated mycorrhizal fungi. Their distribution in the soil defines the soil depth to which uptake can occur (uptake zone). It has been hypothesized that trees with a substantial uptake of nutrients from deep soil layers may deplete the topsoil less than trees with a more shallow root system, since the former may utilize weathering products from the deeper layers (Sverdrup and Stjernquist 2002). Thus has the deep-rooted oak (Rosengren et al. 2005) been suggested to be more nutrient sustainable than more shallow rooted species (Sverdrup and Stjernquist 2002). In this study we have tried to verify if the vertical root distribution is a good estimate of the distribution of nutrient uptake.

It has been assumed that roots of a species in the same size class have the same function (Pregitzer 2002) and thus have a similar uptake capacity. However, it has also been found that the N content and the respiration rate both decreased with depth in roots of the same size in sugar maple (*Acer saccharum* Marsh.; Pregitzer et al. 1998). If the respiration rate differs, it is likely that the nutrient uptake capacity will also differ, which may be of importance for the nutrient uptake capacity of the whole tree. At the same site this has been investigated previously in a study where the trees' nutrient uptake capacity was estimated at different depths by measurements of root and mycorrhiza distribution, and the nutrient uptake of roots sampled at different soil depths using a root bioassay (Göransson et al. 2006b). The capacity of oak roots to take up ^{86}Rb (used as an analogue to K) was found to decline in the fine roots with increasing soil depth and the same trend was found for NH_4. However, the roots of European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) did not differ in nutrient uptake capacity depending on soil depth. The authors found that despite the fact that oaks had more roots at 50 cm soil depth than beech and spruce, the estimated uptake at this depth was lower due to the low uptake capacity of the fine roots (Göransson et al. 2006b). The decline in the oak roots' uptake capacity with increasing soil depths has been verified in 8 oak stands in southern Sweden (Göransson et al. 2007). Thus, one can question whether the ability of trees to take up nutrients from deep soil layers is correlated solely with the distribution of their roots.

Direct measures of the nutrient uptake at different soil depths

The uptake capacity at different soil depths can be estimated by injecting markers for nutrients (isotopes or analogues) and detecting the markers in the biomass. Radioactive isotopes have been used in most cases, mainly radioactive phosphorus ^{32}P and ^{33}P, but also radioactive calcium ^{45}Ca and radioactive rubidium ^{86}Rb (Brandtberg et al. 2004; Göransson et al. 2006a; Harrisson et al. 1988; Nethsinghe and Broeshart 1975; Lehmann et al. 2001; Thomas et al. 1998). The stable isotope ^{15}N has been used to investigate the vertical distribution of uptake in agroforestry and forests in the tropics (Lehmann et al. 2001; Lehmann and Muraoka 2001; Rowe et al. 1999; Rowe et al. 2001; Soethe et al. 2006) and in mixed stands of oak and Norway spruce (Göransson et al. 2006a). Otherwise, ^{15}N has mainly been used in forests to estimate the capacity to take up ^{15}N applied to the soil surface (Buchmann et al. 1995; Gebauer et al. 2000; Genenger et al. 2003; Gundersen 1998; Nadelhoffer et al. 1999; Nömmik and Larsson 1989; Tietema et al. 1998). To estimate the uptake of nutrients such as potassium (K) and Ca, analogues such as lithium (Li), Rb, caesium (Cs) and strontium (Sr) can be used (Fitter 1986; Mamolos et al. 1995; Memon et al. 1983; Yoshida and Muramatsu 1998; Zhu and Smolders 2000). These have mainly been used in the study of smaller plants (Fitter 1986; Mamolos et al. 1995), but we have previously performed a study on mature trees using Cs (Göransson et al. 2006a). In order to estimate the relative contribution of nutrient uptake from a certain soil depth, the dilution of the tracer in the soil as well as the sorption of the tracer to

soil particles should be taken into account (Harrisson et al. 1988). However, the dilution and sorption of markers are usually not compensated for when describing the distribution of nutrient uptake in agroforestry systems in the tropics. Nevertheless, good correlations between root distribution and nutrient uptake are usually found in these studies (Lehmann 2003; Soethe et al. 2006). However, in a boreal forest, Brandtberg et al. (2004) found that Norway spruce had the same capacity to take up Ca and P from a depth of 35 cm in the mineral soil as birch (*Betula* spp.). This occurred even though birch had relatively more fine roots at this depth than Norway spruce indicating a poor correlation between root distribution and nutrient uptake.

The aim of this study was to compare the relative uptake of N and K from soil depths of 5 and 50 cm in deep-rooted oak and beech and shallow-rooted Norway spruce under similar conditions.

Method

Site description

The site is located in Palsgård State Forest District, in the Hastrup Plantation outside Brande, in an agricultural landscape in central Jutland, Denmark. The site is part of a large Danish tree species trail containing 12 tree species repeated at 13 sites throughout Denmark. Three- to four-year-old seedlings, including European beech (*Fagus sylvatica*), Norway spruce (*Picea abies* (L) Karst.) and pedunculate oak (*Quercus robur)* were planted in monocultures in about 0.2 ha plots in 1964–1965. The soil at Palsgård is an anthric podsol of sorted semifine sand with 2–3% clay. The site is considered to be poor in cations due to the coarse material, with a pH ($CaCl_2$) increasing from around 3.4 to 4 with increasing soil depth. (Callesen 2003). Prior to tree planting the site was used for agriculture and had been deep ploughed to a depth of 60 cm (Callesen 2003).

Application of tracer elements

CsCl (300 g) and $(^{15}NH_4)_2SO_4$ (60 g) labelled with ^{15}N (98%) were dissolved in 2400 ml distilled water. Each plot was divided along the diagonal into two subplots. In each subplot 10 trees were selected, spread evenly over the area and at least 8 m from a selected tree in the other subplot. Twenty plastic (PVC) tubes were inserted into pre-bored holes (∅=1 cm) in a circle around each tree, approximately 1 m from the trunk. In one of the subplots the tubes were inserted to a depth of 5 cm in the mineral soil and in the other subplot to 50 cm depth. The labelled solutions were injected into the tubes with a stepper pipette (Finnpipette stepper) on June 17th and 18th, 2003. Each tree received 1 g of $(^{15}NH_4)_2SO_4$ and 5 g of CsCl. After the injections the tubes were flushed with 2 ml distilled water and sealed with adhesive tape. The tubes were removed after 65 days (19th September 2003).

Sampling and analysis

Before the injection of the tracers, foliage from the upper half of the crown of five trees from each plot were collected to obtain background values of Cs. Sixty-five days after injection buds and leaves and needles were sampled by collecting eight branches, including foliage, from all around the upper half of the crown (in spruce around the eighth node from the top and only current year needles). The time of 65 days was shown to be sufficient in the study by Göransson et al. (2006a) and Göransson (2006). The buds, leaves and current-year needles were then dried at 40°C. The dried foliage and buds were milled separately in a ball mill for 10 min to a fine powder. Four to eight milligrams was put in tin capsules and analysed for ^{15}N content and total N content using a mass spectrometer (Europa Scientific) according to Ohlsson and Wallmark (1999). The Cs and K contents were determined by digesting 0.5 g dried sample in concentrated HNO_3 at 125°C. Cs was analysed using ICP-MS (Perkin Elmer, Elan-6000), and K using ICP-AES (Perkin Elmer, OPTIMA 3000 DV).

Estimation of the relative immobilization and dilution of $^{15}NH_4$ in the soil

On 15th of June 2004, soil samples were taken from a depth of 0–11 cm and 44–55 cm from 10 holes evenly spread over each of the oak, spruce and beech plots (1 year after the injection of the ^{15}N and Cs). The soil was stored at 2°C for four days before analysis. To estimate the amount of plant available NH_4, 25 g of soil was extracted in 100 ml 0.1 M $BaCl_2$ for 1 h and filtered. The extract was then frozen before being

analysed for NH_4 using flow injection spectrometry. To estimate the amount of the added ^{15}N that had been absorbed by the soil and immobilized by micro-organisms, samples from 5 out of the 10 holes were used. A total of 25 g of soil from each sample was added to two 30 ml capsules (two sets of 30 capsules). To each capsule 1 ml of 1 mM $^{15}NH_4Cl$ (similar amount as was present in the soil) was added and the soil was then mixed. To estimate the abiotic absorption, one set of capsules was stored at 2°C during the injection of ^{15}N to minimize the microbial activity, and 30 min after injection the samples were extracted in 100 ml 0.1 M $BaCl_2$, filtered and frozen. To estimate the microbial immobilization of $^{15}NH_4$ the other set of capsules was sealed and incubated in darkness at room temperature for 5 days and then maintained at 2°C for 6 days before being extracted. From each capsule 10 g of soil was extracted in 40 ml 0.1 M $BaCl_2$, filtered and frozen. The extract was thawed and 5 ml was vacuum centrifuged without heat to remove the water (Savant AES 1000). The salt remaining after vacuum centrifugation was weighed in tin capsules and analysed using IRMS for ^{15}N content. The water content in the soil was determined by drying at 105°C overnight.

Calculation of the relative K and NH_4 uptake from different soil depths

Potassium is preferentially taken up by the roots, rather than Cs. The degree of discrimination depends on the K concentration in the soil solution. A high K concentration reduces the Cs uptake by the roots (Smolders et al. 1997). Close to the injection point, the concentration of Cs ions will be much higher than the concentration of K ions, resulting in insignificant discrimination against Cs. Further away from this point the concentration of K in relation to Cs will increase, resulting in increasing discrimination against Cs. The discrimination against Cs, assuming K to be dominant over Cs in the soil solution, has been investigated when estimating the plant uptake of the radioactive ^{137}Cs deposited after the Chernobyl accident (Absalom et al. 2001; Absalom et al. 1999; Smolders et al. 1997). The discrimination against Cs under these conditions can be calculated using equation 1:

$$\log(\mathrm{CF}) = k_1 - k_2 \log(m_k) \quad (1)$$

where CF is the concentration factor (CF=Cs conc.$_{plant}$/Cs conc.$_{soil}$), k_1 (5.23) and k_2 (2.42) are empirical constants and $[m_k]$ is the concentration of K in the soil solution. The concentration of K in the soil solution can be estimated from the inorganic cation exchange capacity (CEC) derived from the clay content at the oak site (Callesen 2003) and the extractable K in the soil (Absalom et al. 1999). The extractable K was analysed using the same extract as for background values for NH_4 using ICP-AES (Table 1).

As Cs can be considered an analogue to K, the Cs recovery can be expressed as the increase in the Cs/K ratio above the background (Göransson et al. 2006a). The enrichment of ^{15}N in foliage and buds is expressed as $\delta^{15}N$, where $\delta^{15}N$ was calculated as $1{,}000 \times (\mathrm{atom\%_{sample}} - \mathrm{atom\%_{reference}})/\mathrm{atom\%_{reference}}$. The natural ^{15}N atom% reference is 0.3663%.

Statistics

Two-way ANOVA, with tree species and soil depth as independent factors was used to analyse differences in Cs and ^{15}N recovery in the leaves, needles and buds. The ^{15}N recovery data was log-transformed to obtain normally distributed data. Differences in microbial and chemical immobilization of ^{15}N between soil depths was analysed using a t test.

Results

The amount of Cs recovered in the foliage and buds was similar regardless whether the isotopes had been injected at 5 or 50 cm soil depth in both beech and Norway spruce trees. However, in the oak trees more Cs was recovered from 5 than from 50 cm (foliage P=0.017, buds P=0.034; Fig. 1). This occurred even though oak had relatively more fine roots (∅=0–1 mm) at 50 cm soil depth than at 5 cm (P=0.052 One-Way ANOVA, Tukey, calculated from Göransson et al. (2006b); Fig. 2). The concentration of K in the soil solution, estimated from the amount of extractable K (Table 1), was found to be 181 μM at 5 cm and 106 μM at 50 cm for beech, and 150 μM, at 5 cm and 87 μM at 50 cm soil depth for oak. In the Norway spruce stand, the extractable K concentrations at 50 cm soil depth were too low to allow reliable calculations of the discrimination against Cs. The discrimination against Cs was calculated to be 3.7 times higher at 5 cm than at 50 cm soil depth for

Table 1 Average values (± standard error) of extractable amounts of K and NH_4 in the soil at 0–11 cm and 44–55 cm soil depth (0.1M $BaCl_2$). (n=10)

	K (μg/g)		NH_4 (μg/g)	
	0–11 cm	44–55 cm	0–11 cm	44–55 cm
Beech	9.16±0.39	2.76±0.76	0.53±0.12	0.30±0.06
Oak	6.59±0.39	1.85±0.61	1.42±0.33	0.71±0.10
Spruce	2.08±0.45	0.075±0.06	0.82±0.13	0.49±0.06

both oak and beech where K was dominant over Cs in the soil solution. This means that the uptake of K from 5 cm is underestimated but this does not change the fact that the relative Cs uptake from 50 cm soil depth was lower in oak than in beech (Fig. 2). The uptake from 5 cm in Norway spruce is probably even more underestimated than in oak and beech, as the K concentration was very low at 50 cm soil depth compared with 5 cm, meaning that the relative K uptake from 50 cm soil depth is probably less in spruce than in beech (Fig. 2). These data fit rather well with the estimated uptake capacity at the site found by Göransson et al. (2006b; Fig. 2).

However, due to the high Cs concentrations near the application point the discrimination against Cs by the roots is probably less than that calculated using equation 1. The uptake capacity of K from 50 cm is probably somewhere between the compensated and the not compensated value (Fig. 2). This means that the uptake in beech from 50 cm is between 33 and 100% of the uptake at 5 cm soil depth and for oak between 8 and 24%.

The amount of ^{15}N in both foliage and buds did not differ significantly between the soil depths in any of the tree species although in oak there was a tendency for uptake from 5 cm to be higher than from 50 cm soil depth (Fig. 3). The availability of the ^{15}N injected into the soil was not affected by differences in the chemical properties of the soil, as the abiotic immobilization did not differ between the different soil depths (Fig. 4). The incubation of the soil samples demonstrated that ^{15}N was immobilized by microorganisms (P<0.001, paired t test). The only difference between soil depths after incubation was found in the beech stand, where the soil from 5 cm soil depth had immobilized less ^{15}N than the soil from 50 cm

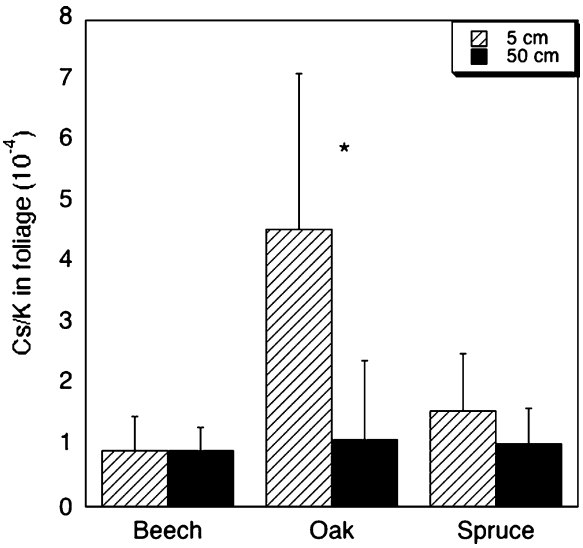

Fig. 1 Uptake of Cs into foliage expressed as the Cs/K concentration ratio. The background values for each species at the site has been subtracted. (n=10, *P<0.05, error bars show St dev)

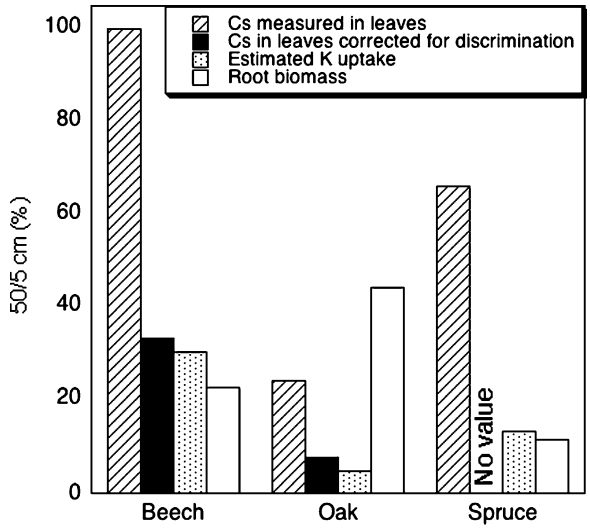

Fig. 2 The uptake capacity of Cs into the foliage at 50 cm soil depth as compared to 5 cm soil depth before and after compensation for discrimination. No value is presented for Cs in Norway spruce due to large uncertainties in the discrimination against Cs. The measured uptake capacity is compared with the values estimated previously for K and the root biomass (∅=0–1 mm; Göransson et al. 2006b)

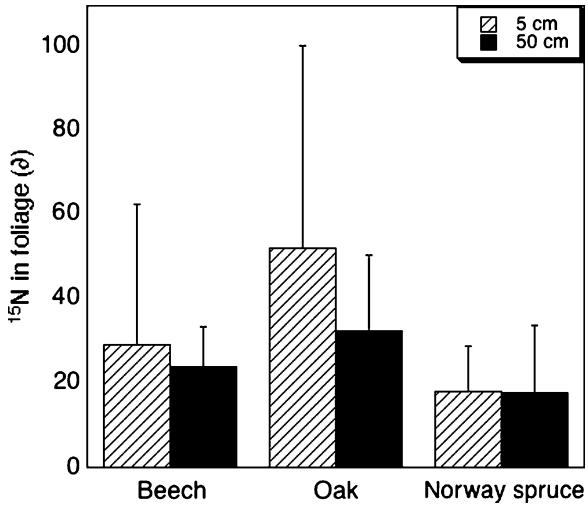

Fig. 3 Uptake of ^{15}N into foliage expressed as ∂ calculated with the atmospheric N isotope ratio as the standard. (n=10, error bars show St dev)

(P<0.01; Fig. 4). The uptake capacity from 5 cm soil depth of beech may thus have been overestimated due to lower microbial immobilization of the added ^{15}N. This, however, does not change the fact that the uptake capacity of NH_4 was similar at both depths for all three tree species. The dilution effect due to differences in NH_4 concentrations in the soil at the different soil depths should only have a minor effect as it is in the range of a μg/g soil and more than 8 mg was added in each tube (Table 1; Soethe et al. 2006).

Discussion

Deep-rooted oaks were not found to take up more nutrients from deep soil layers than more shallow-rooted beeches and spruces. The same findings have been reported for deep-rooted birch and more shallow-rooted Norway spruce by Brandtberg et al. (2004). This may be due to an overcapacity within the root system for the uptake of mobile nutrients. If the distances between the roots and between the hyphae within the root system are small this will lead to an overlap of the uptake zones around the root or hyphae, leading to lower uptake per unit root length (Andrews and Newman 1970; Newman and Andrews 1973). The overcapacity will be greater regarding nutrients with high mobility, such as NO_3, K and NH_4, than for less mobile ions such as P, where the uptake zones around the roots and hyphae probably do not overlap to the same extent. If there is a greater overcapacity in the topsoil than in deep soil layers the relative uptake from the top layer should be lower than that indicated by the relative amount of roots and mycorrhizal mycelium. To estimate the theoretical uptake capacity of for example, K during the duration of the experiment (65 days) it is necessary to know the density of active roots and mycorrhizal mycelium, the diffusion coefficient of the ion in question and the time at which the tracer was added to the soil. Taking the overlapping of root uptake zones into account, the percentage of the soil volume that could be depleted is:

$$100*1 - e^{-\pi Lv2Dt} \quad (2)$$

where Lv is the root density, D the diffusion coefficient of the ion and t the time (Newman and Andrews 1973). Based on root data from a previous study (Göransson et al. 2006b) for the beech stand and on the diffusion coefficient given by Marschner

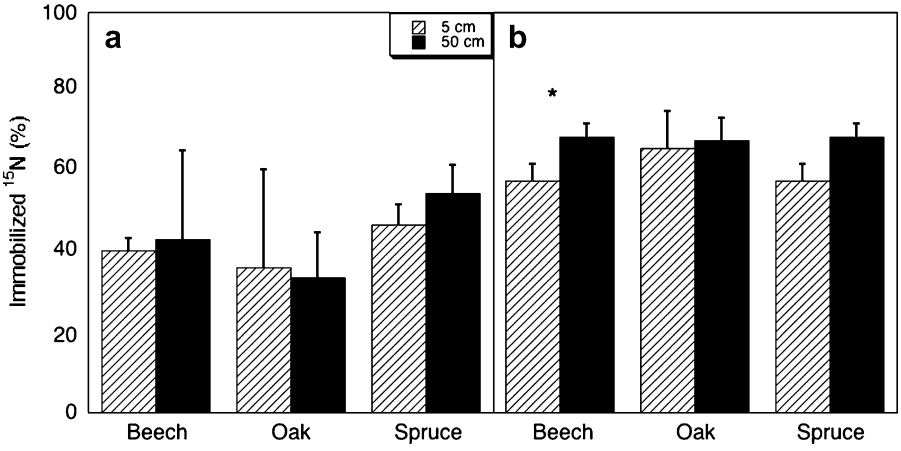

Fig. 4 Immobilization of $^{15}NH_4$ under laboratory conditions. **a** Abiotic immobilization and **b** total immobilization after 5 days' incubation at room temperature. (n=5, *P<0.05, error bars show St dev)

(1986), the theoretical percentage of the soil volume that could be depleted in the mobile K ion in 65 days would be 98% at 0–11 cm soil depth and 76% at 44–55 cm soil depth, assuming that the root uptake is high enough to form a depletion zone around the root. This should be compared with the root length, which at 50 cm soil depth was only 23% of the amount at 5 cm (Göransson et al. 2006b). For the less mobile $H_2PO_4^-$ ion the soil volume depleted would be 11% at 0–11 cm soil depth but only 2.8% at 44–55 cm (based on the diffusion coefficients given by Marschner 1986). Such a difference in relative uptake capacity between different soil depths, depending on the nutrient being studied, has also been reported previously by Göransson et al. (2006a). They found the contribution from 50 cm soil depth to the total uptake in oak from 15 and 50 cm to be 50% for Cs, 25% for ^{15}N and 4% for radioactive P (not compensated for dilution and discrimination). Brandtberg et al. (2004) injected radioactive Ca and P under Norway spruce at 2 and 35 cm depth and found the relative contribution from 35 cm soil depth for Ca to be 14% but only 7% for P (not compensated for dilution).

The low measured uptake capacity from 50 cm soil depth in oak (Figs. 1 and 2) can not be explained by the distribution of roots or external ectomycorrhizal mycelium, as the amounts of roots and external ectomycorrhizal mycelium at 50 cm relative to 5 cm soil depth was higher in oak than in beech and spruce (Fig. 2; Göransson et al. 2006b). The low uptake from 50 cm soil depth is probably due to the low uptake capacity of the fine roots of oak at this depth, previously found in a root bioassay (Göransson et al. 2006b). These authors found that the root uptake capacity in oak was significantly higher at 5 than at 50 cm for Rb (K) and tended to be higher for NH_4 whereas it was similar at both depths in beech and spruce. In this study we found the same pattern with a low uptake capacity of the oak roots in deep soil layers, supporting the notion that differences in functionality of the roots may have consequences for the nutrient status of the whole plant. Zobel (2003) suggests that, 'a plant root system is best described as an integration of multiple genetically and anatomically determined functional root classes'. The bioassay technique may be one way of testing the functionality of the roots, which will take us one step closer to a better description of the root system. Using this method, Rosengren et al. (2003) showed that roots with a smaller diameter were more efficient in taking up N than thicker roots (per g fresh weight), and we found that the soil depth may influence the uptake capacity of the roots (Göransson et al. 2006b). The next aspect to be considered could be the position of the roots on the branching fine root system, which may also influence the nutrient uptake capacity as there seem to be differences in respiration and N content depending on the position (Pregitzer 2002; Pregitzer et al. 2002). However, this would not be sufficient to determine the uptake exactly, as the mycorrhiza must also be considered. Studies in axenic cultures have shown large differences in the nutrient uptake capacity by different mycorrhizal species (Dighton et al. 1993). These differences also affected the actual uptake into the trees in the field (Dighton et al. 1990). As the mycorrhizal community changes with the soil depth, this must also be taken into account when estimating the nutrient uptake capacity at different soil depths (Rosling et al. 2003).

When modelling nutrient uptake in forest ecosystems the capacity to take up nutrients from different soil depths has most often been based on the distribution of the roots (Holmqvist et al. 2002). Changing the depth of the nutrient uptake zone in these models will have a direct influence on the nutrient pools in the soil. Deep-rooted species have thus been considered to be more nutrient sustainable since they were assumed to have greater access to weathering products (Akselsson 2005). It has been assumed in models that oak trees utilize a larger soil volume for nutrient uptake than Norway spruce (Holmqvist et al. 2002). Norway spruce would thus be expected to deplete its available nutrients more quickly than oak, assuming a similar demand by the trees for nutrients. At the site studied here, however, deep roots of oak were relatively less efficient at taking up nutrients than Norway spruce and thus oak was not able to access more weathering products from deeper soil layers than Norway spruce.

Conclusions

The relative contribution of K and N uptake from 50 cm soil depth was higher than would be expected from the root and external ectomycorrhizal mycelium distribution, probably due to a large overlap of the uptake zones within the root system and the external

ectomycorrhizal mycelium for the nutrients in the top layer. However, despite the fact that oak has more roots and external ectomycorrhizal mycelium at 50 cm soil depth than beech and Norway spruce, the relative contribution of Cs from 50 cm soil depth was less for oak than for beech and Norway spruce. This is probably due to low uptake capacity of the roots in deep soil layers, which has been found earlier (Göransson et al. 2006b). Thus, differences in uptake capacity of fine roots at different depths may influence the distribution of nutrient uptake by the tree.

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