Interspecies differences in the preference of ammonium and nitrate in vascular plants

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Abstract Three solution experiments were performed to test the importance of \(\text{NH}_4^+\) versus \(\text{NO}_3^-+\text{NH}_4^+\) to growth of 23 wild-forest and open-land species, using field-relevant soil solution concentrations at pH 4.5. At N concentrations of 1–200 \(\mu\text{M}\) growth increased with increasing N supply in Carex pilulifera, Deschampsia flexuosa, Elymus caninus and Bromus benekenii. Geum urbanum was the most N demanding species and had little growth below 200 \(\mu\text{M}\). The preference for \(\text{NH}_4^+\) or \(\text{NO}_3^-+\text{NH}_4^+\) was tested also at pH 4.0; no antagonism was found between \(\text{NH}_4^+\) and \(\text{H}^+\), as indicated by similar relative growth in both of the N treatments at both pH levels. Growth in solution with \(\text{NH}_4^+\) relative to \(\text{NO}_3^-+\text{NH}_4^+\), 200 \(\mu\text{M}\), was negatively related to the mean pH of the field occurrence of the species tested; acid-tolerant species grew equally well with only \(\text{NH}_4^+\) as with \(\text{NO}_3^-+\text{NH}_4^+\) (Oxalis acetosella, Carex pilulifera, Festuca gigantea, Poa nemoralis, Deschampsia flexuosa, Stellaria holostea, Rumex acetosella), while species of less acid soils were favoured by \(\text{NO}_3^-+\text{NH}_4^+\) (Urtica dioica, Ficaria verna, Melandrium rubrum, Aegopodium podagrigaria, Geum urbanum, Bromus benekenii, Sanguisorba minor, Melica ciliata, Silene rupestris, Viscaria vulgaris, Plantaeg lanceolata). Intermediate species were Convallaria majalis, Elymus caninus, Hordelymus europaeus and Milium effusum. No antagonism between \(\text{NH}_4^+\) and \(\text{Ca}^{2+}\), \(\text{Mg}^{2+}\) and \(\text{K}^+\) was indicated by the total uptake of the elements during the experiment.

Key words Ammonium uptake - Nitrate uptake - Nitrogen preference - Nitrogen mineralization - Vascular plants

Introduction

Nitrogen is mainly taken up as \(\text{NH}_4^+\) and \(\text{NO}_3^-\) by vascular plants and the N form available may be important to the distribution of species. Organic N may be provided by mycorrhizal fungi (Read et al. 1989) and recent studies give examples of species which prefer N supplied as amino acids (Chapin et al. 1993). Mineral N occurs mainly as \(\text{NH}_4^+\) in acidic soils where nitrifiers are absent or restricted. The deposition of 10 kg \(\text{NH}_4^+\) ha\(^{-1}\) year\(^{-1}\) and 10 kg \(\text{NO}_3^-\) ha\(^{-1}\) year\(^{-1}\) to south Swedish forest soils (Westling 1989) is an essential contribution to the total N pool and to the \(\text{NO}_3^-\) availability. Less acid soils transform all mineralized N to \(\text{NO}_3^-\) when studied in laboratory incubation experiments (Runge 1983). Plants may, however, compete with microbes for \(\text{NH}_4^+\), making an uptake of both N forms also possible in nitrifying soils (Jackson et al. 1989; Davidson et al. 1990). It is known that many ectomycorrhizal fungi can utilize \(\text{NO}_3^-\) as well as \(\text{NH}_4^+\) (Read et al. 1989) and this has recently been shown also for arbuscular mycorrhizal fungi (Johansen et al. 1993a, b).

Experiments on the preference for \(\text{NH}_4^+\) and \(\text{NO}_3^-\) have partly given different results. In some solution experiments plant species of acidic soils grew best with \(\text{NH}_4^+\), species from soils of intermediate acidity with a mixture of both N forms and species of neutral soils with \(\text{NO}_3^-\) (Bogner 1968; Rosnitschek-Schimmel 1982; Neitzke 1990). In other experiments acid tolerant species were indifferent or grew best in a mixture of both N forms (Hackett 1965; Gignon and Rorison 1972; Le Tacon et al. 1982; Rorison 1985; Blacquibre et al. 1988; Falkengren-Gerup and Lakkenborg-Kristensen 1994). However, many studies have used unrealistic concentrations of N (>1 mM) and other nutrients, as compared to the soil solution of acid forest soils. Concentrations in percolation water from the topsoil of six moderately acid beech forests in south Sweden were 0.04–0.20 mM \(\text{NH}_4^+\) and 0.20–0.95 mM \(\text{NO}_3^-\) (Falkengren-Gerup 1994). As the ion composition and concentration affect plant performance (Hackett 1965; Klotz and Horst 1988; Falkengren-Gerup and Tyler 1992; Brunet 1994), it is most important to use field realistic solutions, though a translation from field concentrations to a constant flow in a solution is still difficult to make. Other divergences are different mobility of \(\text{NO}_3^-\) and \(\text{NH}_4^+\) in the soil, and the...
absence of a functioning mycorrhiza might also be a problem.

Negative effects of NH$_4^+$ on the rhizosphere may be due to root release of H$^+$ as an exchange for NH$_4^+$, while at NO$_3^-$ uptake an excretion of OH$^-$ may occur. This is probably of minor importance in a flowing solution system with controlled chemical conditions. The uptake of NH$_4^+$ may also decrease the uptake of other cations (Breterler 1973; Kurvits and Kirkby 1980; Chaillou et al. 1986a; Findenegg 1987), and excess uptake of NH$_4^+$ may make demands on the supply of C for synthesis of free amino acids (Blacquiere et al. 1988; Shen et al. 1990; Kpodar et al. 1992). The extra demand on the C supply may be crucial if NH$_4^+$ nutrition also decreases the photosynthetic rate (Kpodar et al. 1992). The ATP cost for the synthesis of amino acids and organic acids in plants supplied with NH$_4^+$, however, may be much lower than in plants supplied with NO$_3^-$ (Chaillou et al. 1986b).

The aim of this study is to examine whether forest and open-land species naturally growing in soils of different acidity have as high or higher growth potential when N is available solely as NH$_4^+$ compared to a mixture of NH$_4^+$ and NO$_3^-$. This problem may have relevance in trying to explain the edaphical distribution of plants.

Materials and methods

Nitrogen mineralization and field distribution of species

A potential (net) N mineralization of soils was studied in an 8-week incubation experiment under constant water and temperature conditions using the topsoil (0–5 cm, litter removed; composite sample of ten cylinders of 192.5 cm$^3$) of 86 well-drained beech and 101 oak forest soils in southern Sweden. Three replicates of 30 g soil were incubated at 60% of maximum water capacity at 20°C. Net N mineralized was estimated as the difference between amounts of NO$_3^+$+NH$_4^+$ (extractable with 0.2 M KCl) at start and after 8 weeks. Cover (%) of field-layer species was estimated as the mean of the vertical projection in ten subplots of 5 m$^2$.

Experiments

Three greenhouse experiments were performed from February 1993 to May 1994 using a flowing solution culture without recirculation composed to simulate soil solutions of acidic forest soils. No Al was included, mainly to avoid introducing a possibly toxic element. The solution experiments were designed to examine the effect on plant growth of four N concentrations within a range measured in acidic forest soils (experiment 1), the possible interactions of H$^+$ and N form (experiment 2) and the preference for NH$_4^+$ and NO$_3^-$ of wild-forest and open-land plants distributed on soils of different soil chemistry (experiment 3). The results from experiment 3 were compared to species distributions in beech and oak forest soils characterized by the percentage of NO$_3^-$ to total mineralized N in the laboratory incubation experiment.

The solution was supplied individually to the bottom of non-transparent plastic 14 vessels at a rate of 2 ml min$^{-1}$ using 25-1 tanks which were refilled each week. In each vessel, drained by overflow, non-transparent polyethylene disks supported plants of different species placed in a random order. The average temperature during the day was 20°C (range 16–24°C) and at night 14°C (range 10–17°C). The greenhouse was situated under a mixture of deciduous and coniferous trees. Additional light was provided 12 h day$^{-1}$ by 400 W Philips Son-T Agro lamps, which yielded 70 W m$^{-2}$ in the 350–800 nm range and 0.12 W m$^{-2}$ in the 250–350 nm range, as measured at the plant surface.

Out of the 23 species studied, 16 originated from deciduous forest and 7 from open land. Seventeen species were grown from seeds and six were taken from the field. Their differing preferences for soil pH are indicated in Table 4. Plants of equal size were used and long roots were cut to 5 cm.

The composition of the solution (in mM) used in all experiments simulated soil solution conditions of acidic forest soils: 0.25 Ca$^{2+}$, 0.20 K$^+$, 0.08 Mg$^{2+}$, 0.20 Na$^+$, 0.005 Fe$^{3+}$ (as citrate), 0.02 Mn$^{2+}$, 0.002 Zn$^{2+}$, 0.2x10$^{-3}$ Cu$^{2+}$, 0.1, 10$^{-3}$ molybdate, 0.005 boric acid, 0.01 phosphate. The NH$_4^+$ treatment held (in mM) 0.20 NH$_4^+$, 0.79 Cl$^-$ and 0.26 SO$_4^{2-}$, the mixed treatment (in mM) 0.05 NH$_4^+$, 0.15 NO$_3^-$, 0.60 Cl$^-$ and 0.20 SO$_4^{2-}$. In an earlier study six out of seven forest species were not favoured by a solution with NO$_3^-$ as the sole N form (Falkenberg-Grenup and Lakkenborg-Kristensen 1994) and this treatment was, therefore, not included. Six replicate vessels of the treatments were randomized. Each vessel supported two plants of five species (experiments 1 and 2) or one plant of six species (experiment 3). pH was measured daily in the vessels and adjusted by addition of NaOH or a mixture of HCl+H$_2$SO$_4$ (3:1) to the storage tanks. A maximum aberration of 0.10 pH-unit was allowed. The experiments were run for 3–8 weeks, dependent on growth. Roots and shoots were separated and dried to constant weight at 40°C. The shoot and new roots were weighed.

Treatment effects were tested by use of Student’s t-test and one-way ANOVA followed by Duncan’s test (P<0.05).

Results

Nitrogen mineralization and field distribution of species

The growth response of 12 species used in experiment 3 was compared to their distribution in beech and oak forests as related to the soil nitrification in the topsoil studied under laboratory conditions. The percentage of NO$_3^-$ out of the total amount of mineralized N varied between 0 and 100 within the intermediate pH range of the soils (pH KCl 3.1–3.7). Ammonium dominated at pH<3.1 and NO$_3^-$ at pH>3.7 (Fig. 1). The variation within a relatively narrow, intermediate pH range may elucidate the importance of NH$_4^+$ and NO$_3^-$ in the field.

Fig. 1 NO$_3^-$ percentage of mineralized nitrogen (mol:mol) measured in an 8-week incubation experiment in the topsoil (0–5 cm) of 86 beech and 101 oak forests. pH was measured in 0.2 M KCl. Groups A–F were used in Table 1.