



## Nitrogen and base cation uptake in seedlings of *Acer pseudoplatanus* and *Calamagrostis villosa* exposed to an acidified environment

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### Abstract

The effects of solution acidity and form of nitrogen on net nutrient uptake rates in *Acer pseudoplatanus* and *Calamagrostis villosa* seedlings were examined as part of a complex ecological study. Uptake rates were measured by the depletion method under controlled conditions (temperature 20 °C, irradiance 400  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR) from a nutrient solution containing 1.5 mM nitrogen in the form of nitrate or ammonium or an equimolar mixture of both. The solution acidity was kept constant at pH 5.5 (control treatment), 4.5 or 3.5 (low pH treatments). Strongly acid pH decreased or stopped the uptake rates of  $\text{NO}_3^-$ ,  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$ , but the uptake of  $\text{NH}_4^+$  was not changed in both species. Ammonium ions reduced the uptake rate of  $\text{NO}_3^-$  in *Acer* but increased the uptake rate in *Calamagrostis*. Ammonium as the sole source of nitrogen had a strong negative impact on the uptake rates of calcium and magnesium and this effect was independent of the media acidification usually connected with  $\text{NH}_4^+$  uptake and assimilation. However, the negative effect of ammonium ions on the base cation uptake was more pronounced at low pH values.

### Introduction

Progressive forest disturbance is one of the most significant ecological problems in central Europe. The rapid expansion of perennial grasses has been observed in many disturbed forests and in open deforested areas. The new grass stands are surprisingly stable for a long period of time and prevent spontaneous reforestation by tree seedlings. In addition to the above-ground competition for light (Gloser, 1996; Gloser and Gloser, 1996), the interactions of tree seedlings and grasses below-ground should be considered.

Low soil pH values are usually found on declining forest sites. However,  $\text{H}^+$  toxicity *per se* is rarely the factor limiting plant growth in these areas (Marschner, 1991). The effect of low soil pH on ion uptake processes, and, consequently, on plant mineral nutrition seems to be more important. The uptake rates of various ions are changed in an acidic environment but not always to the same extent. Thus, the resulting imbal-

ance in the uptake rates of inorganic ions may have a strongly negative effect on plant growth and survival (Oren and Schulze, 1989). Generally, the uptake rates of cations decline with increasing acidity, whereas the uptake of anions is less affected (Marschner, 1995).

The uptake of ammonium ions, which dominate in acidic soils, results in a lower cation/anion ratio of plant biomass. Moreover, the utilisation of  $\text{NH}_4^+$  ions as the main nitrogen source leads to the acidification of the root environment. Changes in the chemical composition of plants following ammonium fertilization are well known (Gijsman, 1990; Raab and Terry, 1995; Troelstra et al., 1995). However, the effects of  $\text{NH}_4^+$  nutrition alone, or in combination with low pH, on the processes of ion uptake are not clearly understood.

The aim of this work was to determine the specific rates of net uptake of selected ions by intact roots of grass and tree seedlings and also the sensitivity of the net uptake rates to low pH and the presence of ammonium ions in the root environment.

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## Materials and methods

### Plant cultivation

Seedlings of the tree species *Acer pseudoplatanus* and perennial grass species *Calamagrostis villosa* were used in our experiments. After germination on fine sand moistened by half-strength nutrient solution, the plants were cultivated in hydroponics in fully controlled conditions. The irradiance was  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR for 14 hours and the day/night air temperature was 20/15 °C. The modified Hoagland nutrient solution contained, in  $\mu\text{M}$  – 603  $\text{Ca}(\text{NO}_3)_2$ , 795  $\text{KNO}_3$ , 190  $\text{KH}_2\text{PO}_4$ , 270  $\text{MgSO}_4$ , 2  $\text{MnSO}_4$ , 0.85  $\text{ZnSO}_4$ , 0.15  $\text{CuSO}_4$ , 20  $\text{H}_3\text{BO}_3$ , 0.25  $\text{Na}_2\text{MoO}_4$ , and 41  $\text{FeNa-EDTA}$ . The solution was renewed each week and its pH was maintained at 5.5. One day before uptake measurements, the experimental plants were transferred to a nutrient solution with lower ionic concentrations ( $500 \mu\text{M}$   $\text{NH}_4\text{NO}_3$ ,  $100 \mu\text{M}$   $\text{CaSO}_4$ ,  $40 \mu\text{M}$   $\text{KH}_2\text{PO}_4$ ).

### Ion uptake measurements

Measurements of ion uptake rates were made by the depletion method with 8 week old plants. The fresh mass of roots reached approx. 0.5 g and 0.2 g for *Calamagrostis* and *Acer* respectively. The sample plants were exposed individually in 80 mL containers filled with aerated nutrient solution. The basic nutrient solution for this measurement ( $190 \mu\text{M}$   $\text{MgSO}_4$ ,  $200 \mu\text{M}$   $\text{CaSO}_4$ ,  $40 \mu\text{M}$   $\text{KH}_2\text{PO}_4$ ) was mixed with either  $\text{NaNO}_3$  or  $(\text{NH}_4)_2\text{SO}_4$  or  $\text{NH}_4\text{NO}_3$  stock solutions to prepare three different nitrogen treatments. The nitrogen concentration at the beginning of the measurement was 1.5 mM in all solutions. The solution pH in each nitrogen treatment was set at 5.5, 4.5 and 3.5 for control and low pH treatments, respectively. The exposure period was 8 h and the pH of the nutrient solution was stabilised by additions of 0.1 M  $\text{H}_2\text{SO}_4$  or  $\text{NaOH}$ . Changes in the concentration of cations in the nutrient solution were determined by capillary isotachopheresis (Isotachopheretic analyser EA 100, LABECO, Spišská Nová Ves, Slovakia). The setup of the analysis was similar to Matejovič (1991). The concentration of  $\text{NO}_3^-$  in solution was determined colorimetrically as described in Cataldo et al. (1975). The roots of the experimental plants were dried (80 °C, 48 h) and uptake rates were expressed on a dry mass basis.

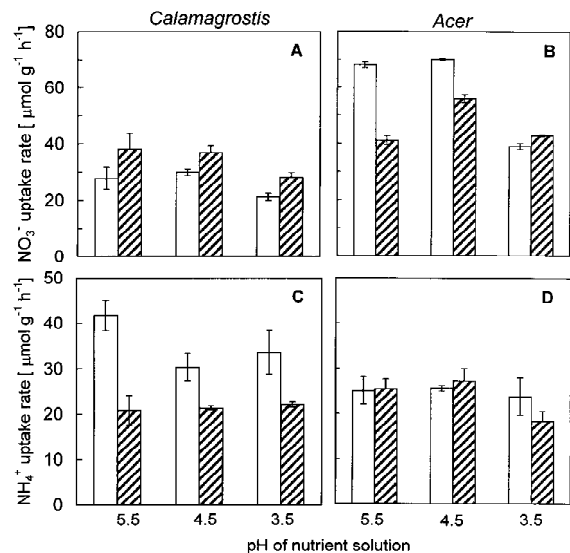


Figure 1. The effect of a sudden decrease of nutrient solution pH on specific net nitrate (A, B) and ammonium (C, D) uptake rates (uptake rate per unit of root dry matter) in *Calamagrostis villosa* and *Acer pseudoplatanus* seedlings. Measurements were made in the presence of either nitrate or ammonium (empty bars) and in the presence of an equimolar mixture of both N forms (dashed bars). The mean values from four measurements  $\pm$  standard error are shown.

## Results

### Uptake rates of inorganic nitrogen

In *Calamagrostis* the specific nitrate uptake rate was only slightly decreased by the low pH of the nutrient solution (Figure 1A, Table 1). The presence of ammonium ions stimulated net uptake of  $\text{NO}_3^-$ . The specific nitrate uptake rate in *Acer* was about two times higher than in *Calamagrostis* (Figure 1B), but it was more sensitive to the low pH of the medium, and significantly inhibited by the presence of ammonium ions in the medium (Table 1, Figure 1B). However, the concomitant presence of ammonium and nitrate in the nutrient solution reduced the negative effect of low pH on nitrate uptake in comparison with the exclusively  $\text{NO}_3^-$  nutrition.

The specific ammonium uptake rate in *Calamagrostis* plants was not affected by the solution acidity (Table 1), but there was a significant decrease in  $\text{NH}_4^+$  uptake in the presence of nitrate. In contrast, *Acer* plants showed no change in ammonium uptake rate either in high  $\text{H}^+$  concentrations or in the presence of  $\text{NO}_3^-$  (Table 1, Figure 1D).

Table 1. The results of ANOVA analysis which tested the effects of solution acidity (pH), form of nitrogen in solution (N- form) and interaction of these factors (pH  $\times$  N-form) on specific uptake rates (uptake rate per unit of root dry matter) of inorganic nutrients in *Calamagrostis villosa* and *Acer pseudoplatanus*. The significance is indicated by \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , n.s. – nonsignificant

Species	<i>Calamagrostis</i>				<i>Acer</i>			
	NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>	NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>
pH	*	n.s.	***	**	***	n.s.	**	***
N- form	**	***	***	**	***	n.s.	***	***
pH $\times$ N- form	n.s.	n.s.	**	*	***	n.s.	**	**

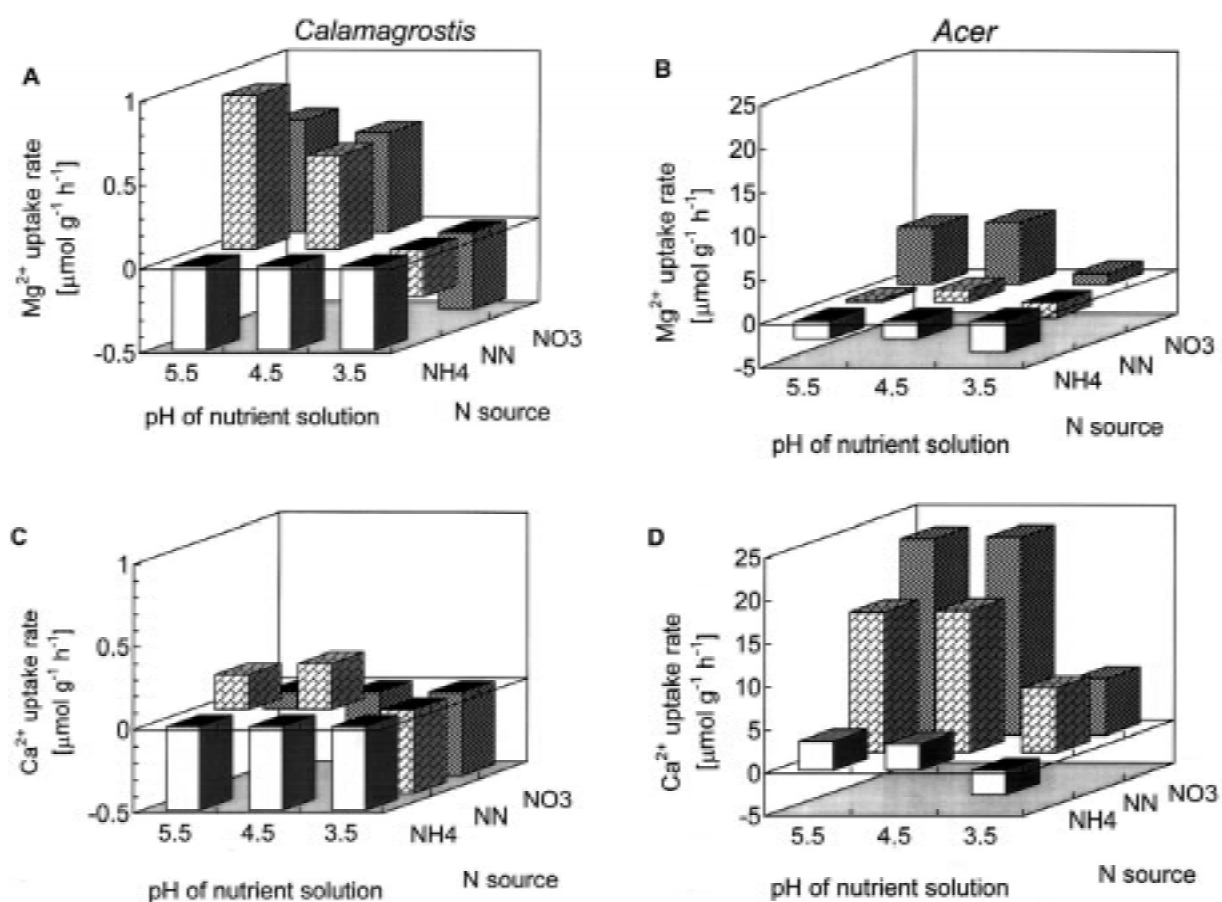


Figure 2. The specific net uptake rates of magnesium (A, B) and calcium (C, D) (uptake rate per unit of root dry matter) in *Calamagrostis villosa* and *Acer pseudoplatanus* seedlings. Nitrogen was present in the nutrient solution in the form of nitrate (NO<sub>3</sub>) or ammonium (NH<sub>4</sub>) or an equimolar mixture of both forms (NN) and the given pH of the solution was kept constant during the measurement. Note, that the scales for the cation uptake rates are different for the two species. The mean values from four measurements are shown. The statistical evaluation of this data is given in Table 1.

### Uptake rates of base cations

The specific uptake rate of magnesium in *Calamagrostis* plants exposed to a solution with pH 4.5 decreased to 80% of the control rate, but at pH 3.5 only a net efflux was recorded (Figure 2A). The concurrent presence of nitrate and ammonium in solution stimulated the  $Mg^{2+}$  uptake rate in comparison with the nitrate treatment when measured at pH 5.5, whereas with ammonium as a sole nitrogen source the net uptake of  $Mg^{2+}$  in all pH treatments stopped. *Acer* seedlings showed almost ten times higher specific uptake rates of  $Mg^{2+}$  than *Calamagrostis*. These interspecific differences were especially large in the nitrate treatment (Figure 2B). *Acer* plants with nitrate as the sole source of N maintained a net uptake of  $Mg^{2+}$  in low pH 3.5, which was remarkably different from the *Calamagrostis* plants. There was, however, no net magnesium uptake in *Acer* plants in solutions with ammonium as the sole source of nitrogen.

The uptake rates of calcium in *Calamagrostis* seedlings were influenced by experimental treatments in a similar way to the uptake of magnesium. Both low pH and  $NH_4^+$  ions as the sole nitrogen source led to a net efflux of  $Ca^{2+}$  from the roots (Figure 2C). The calcium uptake in *Acer* was much faster than in grass seedlings. Both the presence of  $NH_4^+$  and a high  $H^+$  concentration decreased the  $Ca^{2+}$  uptake rate considerably (Figure 2D). However, the net calcium uptake in *Acer* plants was completely stopped only under the combination of ammonium nutrition and pH 3.5.

### Discussion

The experimental technique used in our work allowed us to measure simultaneously changes in the uptake rates of several ions ( $Ca^{2+}$ ,  $Mg^{2+}$ ,  $NH_4^+$ ,  $NO_3^-$ ) under controlled conditions. Much attention was paid to nitrogen, because it is the nutrient with the highest uptake rates and the form in which it is taken up plays an important role in plant ion balance.

The fast uptake and assimilation of nitrate ions is of special importance for plants growing in acidified areas, because these processes are coupled with substantial increases of pH values around the roots. Consequently, the roots may be less threatened by nutrient disharmony and by toxic aluminium ions. The concentration of nitrate ions is usually very low in acidic soils, and, therefore, knowledge of interspecific differences in potential uptake characteristics could be

helpful for the prediction of growth responses and the competitive ability of various species.

### Changes in nitrogen uptake rates

It is generally accepted that the pH of the uptake medium affects the net uptake of  $NO_3^-$  rate by plant roots, but variable responses have been reported. In some plant species, nitrate uptake was highest under acidic conditions (pH 3 to 4) and declined rapidly as the pH was increased (Deane-Drummond, 1984; McClure et al., 1990; Rao and Rains, 1976; Zsoldos and Haunold, 1982). Our results support findings of some other authors that the optimum pH for  $NO_3^-$  uptake may be in some cases much higher (pH 5.5 to 8) (Aslam et al., 1995; Doddema and Telkamp, 1979; Lyclama, 1963). Recently Aslam et al. (1995) used a  $NO_2^-$  incubation technique with barley for separation of the effect of acidic pH on  $NO_3^-$  influx from its effect on efflux. However, Kronzucker et al. (1999) showed on the same plant material that  $NO_3^-$  influx cannot be modelled quantitatively with the use of  $NO_2^-$  as an analogue of  $NO_3^-$ . A study with  $^{13}NO_3^-$  influx in barley at various pH (Glass et al., 1990) showed only small differences between pH 4.5 and 6.0. Nevertheless, these results indicate that the response of nitrate transporters to pH depends on ambient  $NO_3^-$  concentration (cf. pH effect on ammonium uptake).

The specific uptake rate of nitrate in *Acer* was two to three times higher than in *Calamagrostis* plants. Concomitant with higher  $NO_3^-$  uptake rates, nitrate reductase (NR) activity in *Acer* roots was also > 3-fold higher than in *Calamagrostis* (Seidlová 1998). Higher nitrate uptake rates and NR activity per unit of root biomass, however, did not translate into higher growth rate of *Acer* plants (data not shown) primarily due to a much lower ratio of root to whole plant biomass compare to *Calamagrostis*.

In contrast to nitrate, the uptake rate of ammonium ions was not affected by low pH in both species. Results with *Pseudotsuga menziesii* indicate that the rate of  $NH_4^+$  uptake is independent of pH in a range from 3.0 to 6.5 (Rygiewicz et al. 1986). Conversely, the short-term (1 h)  $^{15}NH_4^+$  uptake rate in rice plants was more than 30% reduced under pH 3 compared to pH 6 (Zsoldos and Erdei, 1982) and similar results were obtained during 24 days long cultivation of soybean plants (Tolley-Henry and Raper, 1986). Detailed studies of  $NH_4^+$  uptake in rice found different pH optima for the two ammonium transporters (Wang et al.,

1993). The high affinity transport system mediated the highest uptake rates at about neutral pH, whereas low-affinity transporters attained optimum rates between pH 4.5 and 6.0. Therefore, the response of the net uptake rate to solution pH probably is influenced by the  $\text{NH}_4^+$  concentration in solution, and comparison of data from different experiments should be done with caution.

In the presence of ammonium in nutrient solution, nitrate uptake was decreased in *Acer* seedlings, but it was stimulated in *Calamagrostis* plants. Inhibition of  $\text{NO}_3^-$  uptake in presence of ammonium ions often has been observed (Aslam et al., 1994; Jackson and Volk, 1995; Rao and Rains, 1986) but also stimulation has been reported (Bloom and Sukrapanna, 1990). Short-term  $\text{NH}_4^+$  effects on  $^{13}\text{NO}_3^-$  uptake were recently investigated in barley (Kronzucker et al., 1999). The observed inhibition of net  $\text{NO}_3^-$  uptake in nitrate-induced plants was transient, and mediated primarily by inhibiting  $\text{NO}_3^-$  influx. They proposed that the quick inhibition of  $\text{NO}_3^-$  uptake is connected with a direct effect of  $\text{NH}_4^+$  on the nitrate transport system in plasma membranes and is reversible after withdrawal of ammonium from solution. It seems, thus, unlikely that this direct inhibitory mechanism would cause significant underestimation of  $\text{NO}_3^-$  uptake from  $\text{NH}_4^+$  free solution in our plants which were pre-conditioned in solution containing  $\text{NH}_4^+$  ions. However, it is not possible to exclude completely an after-effect of  $\text{NH}_4^+$  on  $\text{NO}_3^-$  uptake in the plants exposed to  $\text{NH}_4\text{NO}_3$  during 1 day pre-conditioning, e.g. by products of  $\text{NH}_4^+$  assimilation. Nevertheless, our experiments showed clear interspecific differences in sensitivity of  $\text{NO}_3^-$  uptake to  $\text{NH}_4^+$ .

The uptake rate of both  $\text{NO}_3^-$  and  $\text{NH}_4^+$  ions measured in a mixed N treatment were less affected by low pH than the uptake rates of these ions measured in separate  $\text{NO}_3^-$  and  $\text{NH}_4^+$  treatments. There was a higher total N uptake rate recorded in plants grown in a mixed N treatment in comparison with nitrate or ammonium alone. Our results suggest that the beneficial effects of concurrent ammonium and nitrate nutrition, well known from long-term experiments (Vessey et al., 1990; Volk et al., 1992), could be even more pronounced in acidified environments.

#### *Changes in magnesium and calcium uptake*

There is very limited information concerning the uptake rates of base cations obtained by direct measure-

ments of uptake by roots. The lack of experimental work on this topic is partly due to methodological problems and partly because of the complicated interpretation of results.

Decreasing pH of the solution from 5.5 to 4.5 did not dramatically change the uptake rates of base cations in both species. However, after a change of pH from 5.5 to 3.5 there was no net  $\text{Mg}^{2+}$  and  $\text{Ca}^{2+}$  uptake in *Calamagrostis* and a considerably reduced net uptake in *Acer* seedlings. This result is in line with other empirical findings, that the critical pH for plant growth is about 4 (Kennedy, 1992). One possible explanation for this effect is increased competition between base cations and  $\text{H}^+$  ions for binding sites on roots.

A striking difference was found in the specific rates of base cation uptake between *Acer* and *Calamagrostis* seedlings. The *Acer* root system is rather short and thick, whereas *Calamagrostis* has long fine roots with about twice as large absorption area per root dry mass unit than *Acer*. But the specific requirements for base cation supply seems to be much higher in *Acer* plants than in *Calamagrostis*, since the ratio between nitrogen and  $\text{Mg}^{2+}$  or  $\text{Ca}^{2+}$  uptake rates is much higher in grass seedlings. In order to meet the plant's demand for base cations, the less developed roots of *Acer* need to possess much more efficient uptake mechanisms per unit of root surface area than grass seedlings.

The disturbance of membrane integrity in strongly acidic environments is another process which may interfere with the net uptake rates of ions (Zsoldos and Erdei, 1981). The rapid leak of ions from root cells through plasma membranes due to changes in permeability could be an explanation for the relatively high net efflux rates of base cations, which were recorded especially with *Calamagrostis* plants.

The second investigated ecological factor influencing base cation uptake rates was the presence of ammonium ions in the nutrient solution. When ammonium was the sole source of nitrogen, the net uptake rates of base cations were changed in a similar way to exposure of roots to solutions with extremely low pH. Moreover, the adverse impact of  $\text{NH}_4^+$  and high  $\text{H}^+$  concentrations on the base cation uptake rate was additive, so that the combined treatment of  $\text{NH}_4^+$  nutrition and a pH of 3.5 was completely unfavourable for ion uptake in both investigated species. The interference between ammonium ions and base cation uptake often has been explained as an effect mediated by a decrease of rhizosphere pH, which follows  $\text{NH}_4^+$  uptake and assimilation (Gijsman, 1990; Rayar

and Hai, 1977). Our experiments showed an inhibition of base cation uptake when  $\text{NH}_4^+$  was the sole N source even though the solution pH was stabilised at 5.5. This indicates that the influence of ammonium ions on uptake rates of other cations is independent of media acidification. However, the negative impact of ammonium ions on the base cation uptake can be more pronounced at strongly acidic pH.

#### Ecological implications

The reforestation of extensive polluted sites in the Czech Republic with strongly acidic soils is generally considered to be the best landscape management strategy for the future. Broad-leaf tree species including *Acer pseudoplatanus* are more desirable for planting than conifers, because they have a significant ameliorative effect on the soil chemistry (Ulrich, 1987). Any reforestation trial should be based on detailed knowledge of the physiological traits of both the tree seedlings and the competing grasses dominated by *Calamagrostis villosa*. The results of our laboratory experiments can not be, of course, directly applied to field conditions. Nevertheless, the possible ecological implications of our data may show future research prospects.

It is well known that young seedlings of *A. pseudoplatanus* are readily suppressed by grasses, in spite of their extremely high shade tolerance (Jones, 1944). Therefore, our interest was focused on the comparative measurements of nutrient uptake rates under changing environmental conditions, which might be helpful in finding an explanation for interspecific competitive relations within the rhizosphere. At least two physiological traits that can be of potential advantage to the grass *C. villosa* growing on acidic soil can be concluded from our results: (1) its nitrogen uptake rate (both in nitrate and ammonium form) is not markedly depressed even at very low pH, and (2) its demand for base cations is very low, which is also a characteristic of some other grass species (Kinzel, 1982). The second feature may be of special importance, because base cations are very scarce in acidic soils (Schulze, 1989). In such adverse conditions the species with the least requirement will be the superior competitor, as predicted by Tilman's theory of competition (Tilman, 1988).

The relatively high specific uptake rates of the roots of *Acer* are probably not very advantageous in nutrient poor acidic soils, because the relative absorption area of the roots (per DM unit of the whole plant)

is rather low (Hájek, 1998). This is probably why the spontaneous regeneration of *A. pseudoplatanus* is always most successful on nutrient rich soils with a high amount of base cations (Jones, 1944).

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