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The Effect of Liming on the Soluble Nitrogen Pool in Norway Spruce (*Picea abies*) Exposed to High Loads of Nitrogen

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S u m m a r y

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During the growing seasons 1994, 1995 and 1996 the effects of liming of the forest soil on the pools of total soluble non-protein nitrogen (TSNN) in spruce trees (*Picea abies* (L.) Karst) was examined at a field site ('Höglwald', Germany) exposed to high loads of atmospheric nitrogen. For this purpose TSNN contents of fine roots, needles (current and previous year), twig phloem and xylem and root phloem and xylem of spruce trees grown at a plot supplied with 4000 kg calcium magnesium carbonate per ha in March 1994 were compared to untreated control trees. Liming resulted in a transient decrease in TSNN contents in fine roots, root phloem, previous year's needles, and shoot xylem that was most pronounced during the second growing season after liming and that ceased during the third growing season (1996). The observed decrease in TSNN contents in 1995 is attributed to a decrease in ammonium availability that was observed at the field site studied. The re-increase in TSNN contents in the subsequent year is supposed to be a result of changes in the regulation of pedospheric nitrogen uptake that allows the trees to adapt nitrogen absorption to their demand.

I n t r o d u c t i o n

Nitrogen is thought to have been the growth limiting factor in natural forest ecosystems in the pre-industrial time (COLE & RAPP 1981, DICKSON 1989). Human activities have increased the emission of reactive nitrogen compounds (mainly NH_3 and NO) into the atmosphere and, as a consequence, the input of the nitrogen compounds emitted and/or their atmospheric reaction products (e.g. NH_4^+, NO_2, NO_3^-)

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into ecosystems. In Central Europe the patchiness of landscape has resulted in densely populated areas, agricultural land and forests located in close vicinity (RENNENBERG & al. 1998). Thus, many European forest ecosystems are exposed to high loads of NH_3 and NH_4^+ from agricultural sources (ERISMAN & HEIJ 1991, KREUTZER 1995, FANGMEIER & al. 1994, RENNENBERG & al. 1998). These atmospheric nitrogen compounds can be taken up by above-ground parts of plants (BRUMME & al. 1992, PEARSON & STEWART 1993, BURKHARDT & EIDEN 1994, GESSLER & al. 1998c), but the major part is subjected to deposition into the soil where it is available as NH_4^+ for uptake by roots and microbial processes. The uptake of NH_4^+ by roots is connected with a release of protons into the soil solution (MARSCHNER & al. 1991) contributing to soil acidification and, as a consequence, leaching of Mg^{2+}, K^{2+} and Ca^{2+} (ROELOFS & al. 1985, VAN DIJK & al. 1989). The reduction of the availability of these cations may cause or intensify nutrient imbalances within plants (VAN DIJK & al. 1989, ERREBHI & WILLCOX 1990). In order to compensate these adverse effects application of calcium carbonate or calcium magnesium carbonate to forest soil has been carried out in different studies (BINKLEY & HOGBERG 1997, HALLBACKEN & ZHANG 1998, KREUTZER 1995). From these studies it is known that - besides high rates of nitrate leaching (e.g. KREUTZER 1995) - liming generally leads to a long-term decrease in soil acidity, improvement of cation exchange capacity, base saturation and exchangeable Ca^{2+} content (when dolomite is used, also of Mg^{2+}) (HÜTTL & ZÖTTEL 1993, KREUTZER 1995). In spite of these positive effects on soil properties, liming is known not to increase growth of trees (HÜTTL & ZÖTTL 1993, SIKSTROM 1997) or even to have negative effects on yield that are attributed to decreased nutrient availability (SMALLIDGE & LEOPOLD 1997, BINKLEY & HOGBERG 1997). At the field site examined ('Höglwald'), spruce trees are known to meet their pedospheric nitrogen demand exclusively by uptake of ammonium whereas nitrate is not taken up (GESSLER & al. 1998a). Since liming reduces ammonium availability in the soil water (HUBER 1997) and increases competition for this ion between roots and soil microorganisms by stimulating autotrophic nitrification (PAPEN & al. 1994), effects on the nitrogen status of spruce are to be expected. Since neither growth (RÖHLE 1991) of spruce nor total nitrogen content in the needles (HUBER & al. 1998) are influenced by liming at the field site examined, spruce trees are considered to posses mechanisms to cope with changing availability of and competition for nitrogen. It is known that nitrogen uptake by the roots is strongly regulated and adapted to the nitrogen demand of the whole plant (IMSANDE & TOURAINE 1994). A pool of amino compounds cycling between the shoot and the roots is considered to serve as a signal for the plant internal nitrogen status (COOPER & CLARKSON 1989, MULLER & TOURAINE 1992, MULLER & al. 1996, KREUZWIESER & al. 1997).

The aim of the present study was to characterise the effect of liming on the pool of soluble nitrogen compounds (TSNN) in spruce trees exposed to high loads of atmospheric nitrogen. For this purpose TSNN contents were analysed in fine roots, needles, root phloem and xylem and twig phloem and xylem. The TSNN pool is known (1) to react fast on changes in nitrogen availability (GESSLER 1998) and (2) to be involved in the regulation of nitrogen uptake by spruce (RENNENBERG

& GESSLER 1999). Thus, changes in nitrogen uptake caused by altered nitrogen availability and modified regulation of pedospheric nitrogen uptake are supposed to be reflected in the TSNN pools of spruce trees.

Materials and Methods

The studies were performed at the field site 'Höglwald' located 50 km west-north-west of Munich (Germany) at 11°10' E longitude and 48°30' N latitude within the hilly pre-alpine region 540 m above sea level. Climate is suboceanic with an annual average air temperature of 8°C and annual precipitation of 800 m. In 1770 most of the natural vegetation - a submontane Asperullo-Fagetum luzuletosum - was replaced by a spruce plantation. The second generation of spruce has reached an age of 90 yr. in 1997. The trees are apparently healthy; elemental analyses of the needles provided no indications of nutrient deficiencies or imbalances (Rennenberg et al., 1998). The soil of the spruce plantation is an acidic podsolic para brown earth (hapudalf, US soil taxonomy) covered by a moder layer of about 6 cm thickness. The soil is derived from Löss over Tertiary silty sand deposits. The pH(H_2O) is 3.0 to 3.9 in the O-layer; 4.1 -4.2 in the A-layer and 4.2 in the B-layer. Base saturation is 50-80% in the O-layer; 2-5% in the A layer and 20-60% in the B-layer.

A small area of the spruce plantation was limed in March 1994 by application of 4000 kg calcium magnesium carbonate per ha containing 22 kmol Ca and 20 kmol Mg. As a consequence the pH(H_2O) in the O-layer began to increase in autumn 1994 and reached values of up to 4.7 in 1995 to 1997. The pH of the A- and B-layer was not influenced by liming (HUBER & al. 1998). The ammonium concentration in the soil water solution from the O-layer decreased significantly in summer (1995 to 1997) as a consequence of liming. Nitrate concentrations in the soil solutions of O- and A-layer increased in 1994, while the increase in nitrate concentration in the soil solution of the B-layer showed a lag of about one year (HUBER 1997).

Plant material was collected during one field campaign in 1993 and four field campaigns each in 1994, 1995 and 1996. The campaigns were carried out in (I) April (before/during bud break), (II) Mai or June (after bud break) (III) July, and (IV) September at the end of the growing season. Fine roots were dug out from soil in a depth between 0 and 10 cm, washed with double demineralised water to remove adhering soil particles, immediately frozen in liquid N_2, and stored at -80°C. The fine roots of the adult spruce trees were found to be mycorrhizal by visual inspection. Roots of about 1.0 cm diameter were used for the collection of xylem sap and phloem exudates. Twigs were taken from the 7th whorl of spruce. Needles were removed from current and previous year's twig sections, immediately frozen and stored in liquid N_2. 3-4 year old twig sections were used for the collection of xylem sap and phloem exudate.

Xylem sap of twigs and roots was collected immediately after harvest by the modification of the procedure published by SCHOLANDER & al. 1965 described by SCHNEIDER & al. 1996 for twigs and GESSLER & al. 1998b for roots. Contamination with cellular components was checked by measuring luminometrically the ATP content of the xylem sap (SCHUPP 1991) and amounted to <0.5 % in roots and twigs (SCHNEIDER & al. 1996, GESSLER & al. 1998b).

Phloem exudate was collected by the EDTA-technique described by RENNENBERG & al. 1996 and SCHNEIDER & al. 1996. Small pieces of bark (c. 150 mg f.wt) were removed from roots with a diameter of about 1.0 cm and the 3-4 year old twigs. After washing with double demineralised water, the bark pieces were placed in 6 ml vials with 2 ml exudation solution containing 10 mM EDTA and 0.015 mM chloramphenicol at pH 7.0 for 5 hours. Phloem exudates were frozen in liquid N_2 and stored at -80°C until analysis. Previous studies (SCHNEIDER & al. 1996) showed that contamination of phloem exudates of spruce with cellular constituents can be neglected under the experimental conditions applied.

Nitrogen compounds were extracted from needles and fine roots as described by WINTER & al. 1992. Needle and root samples were frozen in liquid N_2 and ground with mortar and pestle. Aliquots of 0.3 g of the frozen powder were homogenised in 0.4 ml buffer containing 20 mM Hepes (pH 7.0), 5 mM EGTA, 10 mM NaF and 2.5 ml chloroform:methanol (1.5/3.5, v/v). The homoge-

nate was incubated for 30 min at 4°C. Subsequently, water-soluble metabolites were extracted twice with 3 ml double demineralised water. The aqueous phases were combined and freeze-dried (Alpha 2-4, Christ, Osterode, Germany). The dried material was dissolved in 1 ml bidistilled H_2O or 1 ml lithium citrate buffer (0.2 M, pH 2.2) for nitrate and amino acid analysis, respectively.

Concentrations of amino compounds and ammonium in phloem, xylem of twigs and roots as well as in the fine roots and needles were determined according to SCHNEIDER & al. 1996 and GESSLER & al. 1998b using an automated amino acid analyser. Nitrate in xylem sap, needle and fine root extracts was detected using ion exchange chromatography combined with a conductivity detector modul (DX-100/120 + CDM, Dionx, Idstein, Germany). In phloem exudates a UV-VIS detector (SPD-6AV, Shimadzu, Duisburg, Germany) was used to detect nitrate after ion-exchange chromatography (SCHNEIDER & al. 1996, GESSLER & al. 1998b). The sum of nitrogen in all amino acids detected, in ammonium and in nitrate was referred to as TSNN. Nitrat and ammonium contents amounted to between <0.1 and 40% of TSNN. Highest amounts were found in the phloem; nitrate and ammonium contents were always very low in fine roots and xylem. Polyamines did not contribute significantly to TSNN (GESSLER 1998).

For xylem sap and phloem exudate analysis of twigs 3 spruce trees were sampled. Xylem sap was collected from three twigs of each tree. Samples obtained from each tree were pooled. Phloem exudates were collected from two twigs of each tree and were analysed separately. For analysis of the needles two further twigs of each tree were harvested and needles of each twig were analysed separately. Data were subjected to Student's *t*-test in order to compare trees from the limed plot with controls. For root phloem exudate and fine root analyses 3 to 5 roots were sampled each. Analyses of amino compounds, ammonium and nitrate of fine roots was performed in 3 to 5 independent samples. Means were compared between samples from the limed site and from the control plot using Student's *t*-test. For the analyses of xylem sap two roots of each treatment were sampled at each campaign in 1994 and 1995 with the exception of June 1995, when 5 roots were collected. In 1996 5 roots were collected for analyses of xylem sap.

Results

In previous year's needles (Fig. 1) of spruce trees from the control plots TSNN contents amounted to 9.1 µmol N g^{-1} f.wt. in April 1994 immediately before bud break and declined significantly until May 1994 (2.0 µmol N g^{-1} f.wt). In July the TSNN content in the previous year's needles increased to 11.4 µmol N g^{-1} f.wt and remained more or less constant until the end of the growing season. In April 1995 the TSNN contents in the previous year's needles of the trees from the untreated control site was significantly higher than in April 1994 amounting to 18.9 µmol N g^{-1} f.wt After decreasing by 76% between April and June 1995 TSNN increased constantly until autumn and reached a value of 11.2 µmol g^{-1} f.wt in September 1995 that was comparable to the previous year. In April and May 1996 the seasonal course of TSNN was comparable to that observed in 1996. In July and September 1996, however, TSNN did not increase like in the two years before but decreased to the lowest level (0.8 µmol N g^{-1} f.wt) observed during the three years examined. The seasonal courses of TSNN in the spruce from the limed plot was similar to the control in 1995 and 1996 but differed significantly in July and September 1994 (Fig. 1). The TSNN contents amounted to 4.1 and 3.6 µmol g^{-1} f.wt in July and September 1994 and were about 64% lower as compared to the control.

In May 1994 TSNN contents in the current year's needles of the control trees (Fig. 1) amounted to 7.9 µmol N g^{-1} f.wt, showed a slight decrease in midsummer and then increased slightly until the end of the growing season in Septem-

ber (8.9 µmol N g^{-1} f.wt). In the next year, TSNN contents of the current year's needles amounted to 4.2 µmol N g^{-1} f.wt. after bud break and increased 3-fold until September 1995. TSNN contents in May 1996 were similar to those of 1995 but decreased significantly in summer (1.0 µmol N g^{-1} f.wt) and in autumn reached a value lower than observed in the two years before (4.2 µmol N g^{-1} f.wt). In May 1994 there was no difference in TSNN contents of the current year's needles between trees from the control plot and from the limed plot. Until the end of the growing season 1995 TSNN contents were slightly lower in the limed trees but this difference was not statistically significant (Fig. 1). In May 1995, however, TSNN contents in the current year's needles exceeded those of controls by factor 2.7. In July and September of the same year TSNN contents did not differ between control trees and trees from the limed plot.

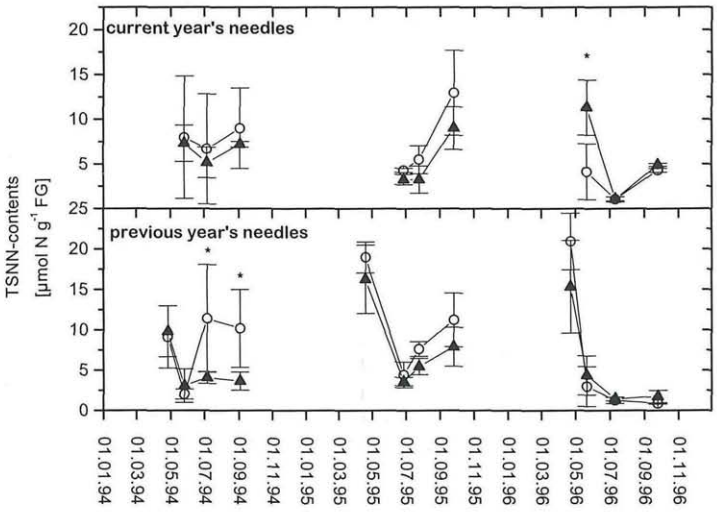

Fig. 1. TSNN contents of current and previous year's needles from adult spruce trees from the plot limed in 1994 (ò) and from untreated control plots (ç). Needles were collected from the seventh whorl and immediately frozen in liquid N_2. Contents of nitrogen in amino compounds, ammonium and nitrate were determined as described in 'Materials and Methods'. Data shown are means of three trees with two replicates each. * indicates significant differences between treatment and control at $p < 0.05$.

During the growing seasons in 1994 and 1995 the seasonal patterns of TSNN contents in fine roots from control trees were similar (Fig. 2). They decreased from May to early summer when a seasonal minimum (8.7 µmol N g^{-1} f.wt in 1994 and 9.2 µmol N g^{-1} f.wt in 1995) was observed. Until July TSNN contents increased c. 3-fold and amounted to 26.7 and 23.7 µmol N g^{-1} f.wt in September 1994 and 1995, respectively. In April 1995 TSNN in fine roots of control trees amounted to 23.8 µmol N g^{-1} f.wt and decreased constantly until the end of the growing season. In September 1995 TSNN contents amounted to 1.4 µmol N g^{-1}

f.wt, the lowest value observed in this study. During 1994 no difference in TSNN contents between fine roots of trees from the limed plot and controls could be observed. However, in 1995 TSNN contents in the fine roots of spruce trees from the limed plots were significantly lower in May, July and September as compared to the controls. In 1996 significant lower fine root TSNN contents in the limed trees could be observed only in April. After bud break until the end of the growing season comparable TSNN content were observed in spruce fine roots from both plots, calcium magnesium carbonate treatment and control.

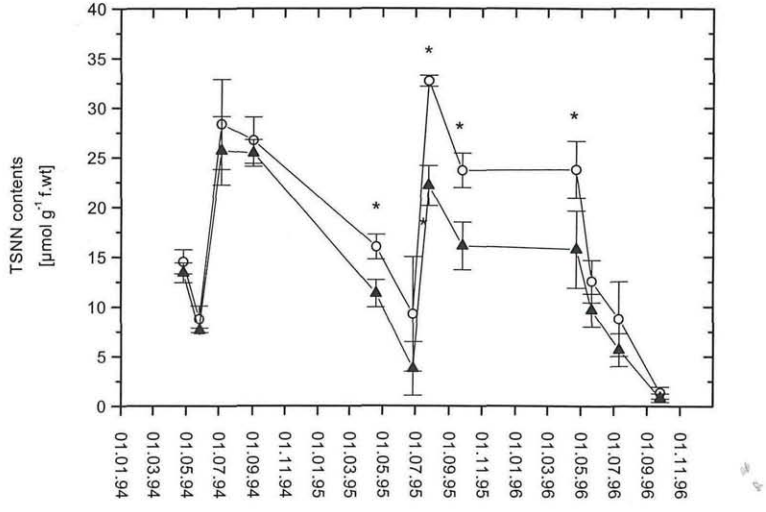

Fig. 2. TSNN contents of fine roots from adult spruce trees from the limed plot (ò) and from the untreated control plot (ç). Fine roots were dug out from depths between 0 and 10 cm. The data shown are means of three to five independent root samples with two replicates analyses, each. Significant differences between treatment and control ($p < 0.05$) are indicated with an asterisk.

In April 1994 before bud break, TSNN contents in the twig phloem of control trees amounted to 13.1 µmol g^{-1} f.wt and decreased significantly to 4.7 µmol N g^{-1} f.wt until May (Fig. 3A). In July and September 1994 TSNN contents reached values of 9.8 and 9.4 µmol N g^{-1} f.wt. Comparable seasonal patterns with decreasing TSNN contents after bud break and increasing contents during midsummer could be observed in 1995. In 1996 the decrease in TSNN contents of twig phloem continued until July when a value of 3.1 µmol g^{-1} f.wt. was detected. In September TSNN contents in the phloem amounted to 4.3 µmol g^{-1} f.wt. In 1994 when calcium magnesium carbonate was applied significant difference in TSNN contents of the twig phloem could not be observed between the spruce trees from the limed plot and the controls. In 1995 significant higher TSNN contents were observed in April - immediately before bud break - in the trees growing on the plots supplied with carbonate. The same observation was made in April 1996 when TSNN con-

tents in the twig phloem of the trees from limed plots exceeded those of control trees by c. 50%. In the subsequent summer and autumn TSNN contents in the of trees from the limed plot was comparable to those of control trees.

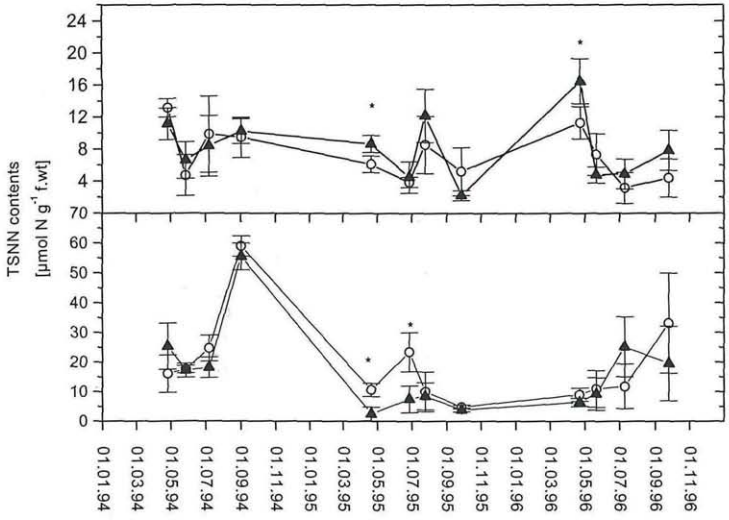

Fig. 3. TSNN contents in phloem exudates from twigs (A) and roots (B) of adult spruce trees from the limed plot (ò) and from the untreated control (ç). The phloem exudate of bark pieces was extracted for 5 h in 2 ml of a solution containing 10 mM EDTA and 0.015 mM chloramphenicol at pH 7.0. TSNN contents were determined as described in 'Material and Methods'. Data shown in (A) are means ± SD of three trees with two replicates, each. The data displayed in (B) are means of three to five root samples with two replicate analyses each. * indicates significant differences between treatment and control at $p < 0.05$.

In April 1994 TSNN contents in the root phloem amounted to 16.1 µmol N g^{-1} f.wt and increased to 59 µmol N g^{-1} f.wt until the end of the growing season (Fig. 3B). Before bud break in 1995 the TSNN values in the root phloem amounted to 10.6 µmol N g^{-1} f.wt, reached a seasonal maximum (23.4 µmol N g^{-1} f.wt) in June and declined until November to 4.8 µmol N g^{-1} f.wt. In 1996 TSNN in the root phloem of control trees remained ± constant between April and June and increased significantly until the end of the growing season (33.1 µmol N g^{-1} f.wt). During the first growing season after the addition of calcium magnesium carbonate (1994) no differences between trees from limed plots and controls were observed. In April and June 1995 TSNN contents in the root phloem of trees from the limed plots amounted to c. 22% and 31%, respectively, of controls whereas in midsummer and autumn 1995 differences did not appear. In 1996 the TSNN contents in the root phloem were similar in treatment and control during all four dates of measurement.

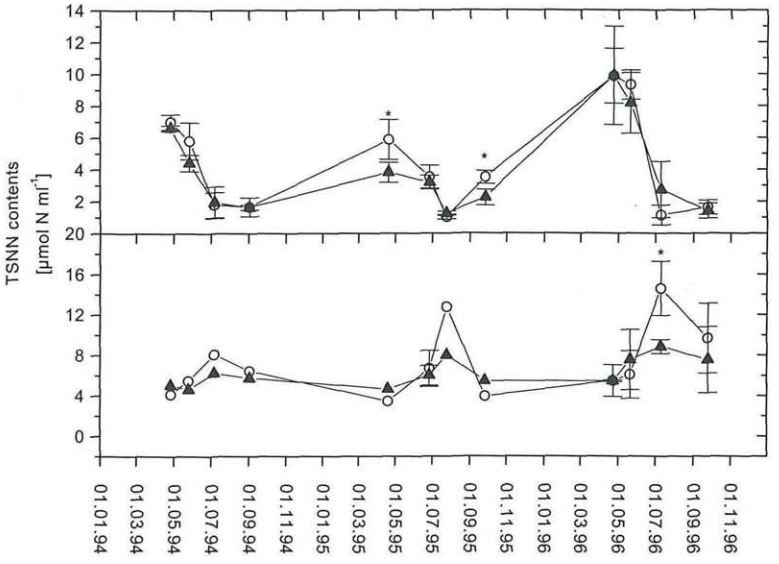

Fig. 4. TSNN contents of twig (A) and root (B) xylem of spruce trees from the limed plot (ò) and from the untreated control plot (ç). Xylem sap was collected from roots and twigs by a modification of the technique described by SCHOLANDER & al. 1965. Data showed in (A) are means ± SD of three trees with two replicates each. For the trials conducted in 1994 and in April, July and September 1995 means of two root samples for each treatment are shown in (B). The data shown for June 1995 and for 1996 are means of five samples, each. * indicates significant differences between treatment and control at $p < 0.05$.

The seasonal courses of TSNN contents in the twig phloem of control trees was comparable between the three years examined (Fig. 4A). The seasonal maximum was observed before bud break in April. TSNN contents amounted to 7.0, 5.9 and 9.8 µmol N ml^{-1} in April 1994, 1995 and 1996, respectively. TSNN contents decreased in all three years between May and August amounting to 1.1 to 1.8 µmol N ml^{-1} in mid summer. In September 1995 and 1996 a subsequent increase in TSNN contents could be observed until the end of the vegetation period, whilst the value in September 1994 remained constant at the level detected in August. Liming had no significant effect on TSNN contents in 1994 and 1996. In April and September 1995, TSNN contents in trees from the limed plot were significantly lower as compared to controls amounting to 4.0 and 2.2 µmol N ml^{-1}, respectively.

Fig. 4B shows the TSNN contents in the root xylem of trees from the limed plot and the control plot between April 1994 and September 1996. In 1994 and during the field campaigns in April, July and September 1995 xylem samples were collected from two roots of each treatment. For the campaigns in June 1995 and for the whole year 1996, the data shown represent means ± SD of 5 independent samples from 5 roots. During all three years examined TSNN contents of root xylem showed comparable seasonal courses in the control trees. A seasonal minimum

was observed in April before bud break. TSNN contents increased between April and August and then declined until the end of the vegetation period.

There was a tendency to lower TSNN contents in the root xylem in trees from the limed plot compared to controls each year in August. In 1995 when xylem saps of five roots were sampled a statistical significant difference between treatments could be observed.

Discussion

In the present study the influence of liming on TSNN contents in xylem and phloem of roots and shoots as well as in extracts of fine roots and needles of spruce trees (*P. abies*) were examined at a field site exposed to high loads of nitrogen due to its close vicinity to intensive agriculture (GÖTTLEIN & KREUTZER 1991). TSNN includes nitrate and ammonium - the inorganic nitrogen compounds taken up by the roots - and soluble amino acids - the primary assimilation products. Therefore, TSNN contents react fast on changes in nitrogen availability, uptake, assimilation, remobilisation and demand (GESSLER 1998) and, thus, can be used for characterisation of the nitrogen status of trees (SCHNEIDER & al. 1996, GESSLER & al. 1998b).

In all three years examined TSNN contents in trees from the control plot and from the limed site showed a marked decrease during bud break (Fig. 1) supporting previous findings that soluble nitrogen that is stored mainly as Arg (FLAIG & MOHR 1992, GEZELIUS & NÄSHOLM 1993) and/or proteins such as ribulose bisphosphate carboxylase (MILLARD 1988) in the previous year's needles is remobilised in spring in order to supply the new flush (MILLARD & PROE 1992, SCHNEIDER & al. 1996, GESSLER & al. 1998b). The increase of TSNN contents in the current year's needles at the end of the growing season observed during the three years of this study indicates the beginning of nitrogen storage within this organ (GESSLER & al. 1998b). In 1994 and 1995 a comparable increase of TSNN was also observed in the last year's needles (Fig. 1) suggesting that they also contributed to nitrogen storage and remobilization in the subsequent year as previously observed by BAUER & al. 1997. However, a TSNN increase in autumn could not be detected in last year's needles of trees from the limed plot in 1994 and in trees from both treatments in 1996. Therefore, it may be assumed that plant internal or external factors can prevent reallocation of nitrogen to older needles in autumn whilst the current year's needles are further supplied with nitrogen for storage. Spruce trees at the field site 'Höglwald' preferentially take up ammonium from the soil whereas the uptake of nitrate is negligible (GESSLER & al. 1998a, RENNENBERG & al. 1998). It may be assumed that decreased availability of ammonium in the soil water and a subsequent drop in nitrogen uptake is responsible for the storage patterns observed since (1) in autumn 1994 a significant reduction of ammonium in the soil water was observed as a consequence of liming (HUBER 1997) and (2) ammonium concentrations even on the control plot were very low in autumn 1996 as compared to the two years before (HUBER 1997). However, TSNN concentrations in fine roots and xylem did not reflect the differences in soil ammonium concentra-

tions between treatment and control at the end of the first growing season. More detailed investigations are necessary to relate possible effects of altered nitrogen availability and uptake to nitrogen partitioning in autumn.

TSNN contents in fine roots did not differ between calcium magnesium carbonate treatment and control during the first growing season, but were significantly lower in trees from the limed plot in April 1995 (Fig. 2). At this time, immediately at the beginning of the growing season, nitrogen uptake by roots was found to be of minor significance (MILLARD 1996, GESSLER & al. 1998a). Therefore, the differences in soluble nitrogen of fine roots and root phloem between trees from limed plots and control plots during early spring may be attributed to differences in nitrogen mobilisation from storage tissues. The increase of TSNN in the fine roots of spruce in summer and autumn 1995 that was observed in both, treatment and control, may be due to an enhanced nitrogen uptake and assimilation (GESSLER & al. 1998b). Lower TSNN contents in the fine roots of trees from the limed plot (Fig. 2) may indicate a less pronounced increase in nitrogen uptake caused by a reduced pedospheric nitrogen supply. This conclusion is consistent with the observation of decreasing ammonium contents in the soil water as a consequence of liming (HUBER & al. 1998). In addition, the pH increase favours propagation and activity of autotrophic nitrifying bacteria (PAPEN & al. 1994) and, thus, may intensify competition for ammonium between soil microorganisms and plant roots. Since liming is known to stimulate fine root growth in the upper soil layer (HÜTTL & ZÖTTL 1993) the redistribution of roots (KREUTZER 1995) together with changing populations of mycorrhizal fungi (QIAN & al. 1998) may also influence TSNN contents in fine roots.

A supposed decrease in ammonium availability of trees from the limed plots can also explain the significant lower concentrations of TSNN in the xylem sap (Figs. 4A and 4B) observed in 1995. However, TSNN contents in the phloem of twigs were higher in trees from the limed plot as compared to controls in spring 1995 and 1996 (Fig. 3A). This finding may indicate increased transport of nitrogen to the developing new flush that is thought to be supplied at least partially via phloem (SCHUPP & RENNENBERG 1992, SCHNEIDER & al. 1994, SCHNEIDER & al. 1996, GESSLER & al. 1998b). At least in 1996 this supposed increase in nitrogen allocation resulted in higher TSNN contents - as compared to controls - in current year's needles after bud break (Fig. 1).

While the TSNN contents in fine roots differed in April, July and September 1995 between treatment and control, in 1996 a significant difference could only be observed immediately before bud break (Fig. 2). Differences in TSNN contents between treatment and control were also no longer observed in the phloem of roots and in the twig xylem in 1996, whereas the differences in root xylem were comparable to the year before.

At the field site 'Höglwald' liming apparently resulted in a transient reduction of the TSNN pool of spruce that is supposed to be caused by the reduction of the ammonium availability in the soil solution. The TSNN pool within the plant is considered to fulfil different functions such as allocation of nitrogen from the sites of assimilation to the sites of consumption and/or storage and adaptation of the

nitrogen uptake to the plants demand (IMSANDE & TOURAINE 1994). The latter task of the TSNN pool may be responsible for the ceasing liming effect on the TSNN pools during the third growing season after calcium magnesium carbonate application. It may be assumed that the decrease in the cycling pool of TSNN in the second growing season after liming can act as signal for the plant to change the regulatory status of nitrate uptake by the roots. Thus, an additional supply of pedospheric nitrate in spruce from the limed plot could compensate for the decreased availability of ammonium. For beech trees at the same field site it was observed that decreased TSNN contents in the fine roots caused by an increased nitrogen demand for beech nut production resulted in nitrate uptake that was not detected during other years (RENNENBERG & GESSLER 1999). The ability of trees to adapt nitrogen uptake to their demand as it was observed in different laboratory (COOPER & CLARKSON 1989, MULLER & TOURAINE 1992, MULLER & al. 1996, CLEMENT & al. 1997, GESSLER & al. 1998c) and field experiments (GESSLER & al. 1998a, b, RENNENBERG & GESSLER 1999) may explain the TSNN patterns observed in this study. Hence, the nitrogen status of spruce is altered only temporary by liming and, therefore, neither total nitrogen contents in needles of spruce at the field site 'Höglwald' (HUBER & al. 1998) nor tree growth (RÖHLE 1991) are influenced by the application of calcium magnesium carbonate.

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