

Effects of nitrogen on tree recruitment in a temperate montane forest as analysed by measured variables and Ellenberg indicator values

Vliv dusíku na vzházení stromů v temperátním horském lese: srovnání přímých měření a Ellenbergových indikačních hodnot

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The UNECE-ICP Integrated Monitoring site Zöbelboden in the Northern Alps of Austria was established to assess the effects of air pollutants on forest ecosystems. Changes in recruitment of the dominant tree species may be among these effects but there is little information on how germination and juvenile growth of these species respond to changes in nutrient supply. This study focused on the effects of nitrogen availability on the performance of the early life history stages of *Picea abies*, *Fagus sylvatica*, *Fraxinus excelsior* and *Acer pseudoplatanus* based on measured soil variables and Ellenberg indicator values. For 106, 0.5 × 0.5 m plots, the pH-value, NH₄⁺, NO₃⁻, gross and net N mineralization and C:N ratio of the top mineral soil were analyzed. Additionally, incoming solar radiation and estimated number of seeds arriving in each plot were recorded. Recruitment and juvenile growth rates of the tree species were related to these variables and to mean Ellenberg indicator values calculated from the vascular plant species composition of the plots, respectively, using linear or generalized linear mixed models. Despite the relatively high correlations of Ellenberg indicator values with the three measured soil variables, namely pH, ammonium, and, in particular, gross N mineralization, models using measured variables and Ellenberg indicator values produced inconsistent results in most cases. In general, closer correlations were obtained between measured soil variables and tree performance than between Ellenberg indicator values and tree performance. Measured nitrogen variables had a significant effect on the recruitment and growth of *Fagus sylvatica* and *Acer pseudoplatanus*. However, whereas the growth of both species was similarly greater where NH₄ contents and gross mineralization rates were higher, their responses to soil nitrogen were clearly distinct in terms of recruitment. Finally, neither recruitment nor growth of *Fraxinus excelsior* are significantly correlated with any of the measured nitrogen variables. Partitioning of regeneration niches in terms of different nitrogen sources and supply rates might hence contribute to the co-existence of different tree species in such mixed mountain forests.

Key words: ammonium, calcareous soils, C:N ratio, gross and net N mineralization, microbial activity, niche partitioning, nitrate

Introduction

Human emissions of reactive nitrogen (N) into the atmosphere have increased tremendously during the 19th and 20th century. The consequential rise in airborne N deposition may have severe effects on ecosystem properties and processes (Fenn et al. 1998, Flückiger & Braun 1998, Erisman & De Vries 2000). Inter alia, changing soil nutrient balances may affect the structure and composition of plant communities by altering the suitability of sites and competitive hierarchies among plant species (Brunet et al. 1998, Diekmann et al. 1999, Van Dobben et al. 1999, Gilliam 2006, Hülber et al. 2008, Seidling & Fischer 2008). In temperate forest ecosystems alterations in the species composition of the overstorey is likely to be driven by differential effects of eutrophication on regeneration, i.e. the germination, seedling survival and juvenile growth, of individual tree species. Indeed, nitrogen decreases the rates of recruitment of trees in early successional plant communities (Henry et al. 2004), affects seedling survival of several tree species (Catovsky & Bazzaz 2000, Sefcik et al. 2007), especially those of mid-successional stages (Catovsky & Bazzaz 2002) and may also affect the growth rates of tree seedlings (Falkengren-Grerup 1995a, Emmett 1999, Leuschner & Rode 1999, Walters & Reich 2000, De Vries et al. 2006, Diwold et al. 2010).

Analyses of the response of plants to environmental gradients are usually based on the occurrence of plant species or their abundance and measurements of abiotic factors. Alternatively, environmental factors may be replaced by indices calculated from plant species composition and species-specific indicator values (Diekmann 2003). The most prominent of these indicator values, namely those of Ellenberg et al. (1992), are frequently used in European studies on vegetation (Diekmann & Dupré 1997, Käfer & Witte 2004). Indeed, such averaged indicator values have advantages: they integrate the effects of several different environmental variables that are not easily measured individually (Dierschke 1994, Wagner et al. 2007) or reflect spatio-temporal variation in long-term resource supply more reliably than a few selective soil samples taken at a particular date (Diekmann 2003, Käfer & Witte 2004, Wagner et al. 2007). Nevertheless, the use of Ellenberg's indicator values in plant ecology is criticized because these indices rest upon expert judgements instead of measurements (Diekmann & Falkengren-Grerup 1998, Diekmann 2003, Wamelink et al. 2005) and refer to the ecological optimum disregarding the width of the ecological niche of the species (Dierschke 1994, Diekmann 2003, Wamelink et al. 2005).

Among Ellenberg's indicator values, the nitrogen index N is still considered the most controversial one (Dierschke 1994, Diekmann & Dupré 1997, Diekmann & Falkengren-Grerup 1998). For example, there is not a close correlation between mean Ellenberg's N and soil nitrogen content in different ecosystems in the Netherlands (Ertsen et al., 1998), and, recently, Smart et al. (2010) have shown that mean values of the nitrogen index are best predicted by a combination of soil moisture content, soil pH, percentage organic carbon and percentage organic nitrogen. Hence, mean Ellenberg's N seems to correlate with different variables and is thus difficult to interpret (e.g. Diekmann 2003). Moreover, the occurrence and abundance of plant species may be less determined by total nitrogen concentration than by the relative availability of inorganic nitrogen ions, such as either nitrate or ammonium (Dierschke 1994).

This study focused on the effects of abiotic gradients, in particular that of nitrogen, on the recruitment and growth of juveniles of the four predominant tree species in a montane

forest in the Northern Limestone Alps in Austria. Analyses are based on both measurements of abiotic factors and unweighted averages of Ellenberg indicator values, and the direct comparison of these alternative approaches, as recommended by Diekmann (2003). Apart from “classical” parameters describing soil nitrogen, gross and net nitrogen mineralization from ^{15}N pool dilution measurements were also used. The expectation was that there would be (i) significant, but differential effects of the different nitrogen parameters on the individual tree species; (ii) variation in the response of different vital rates (recruitment and juvenile growth) to soil nitrogen; (iii) and at least a qualitative agreement among the results of the two different approaches (measured values versus indicator values).

Methods

Study area

The long-term ecosystem monitoring site at Zöbelböden (approximately 90 ha) is part of the UN-ECE ICP-IM (United Nations Economic Commission of Europe’s International Cooperative Programme on ‘Integrated Monitoring of Air Pollution Effects on Ecosystems’) and the Austrian Long-term Ecosystem Research Network (LTER-Austria) (www.umweltbundesamt.at/im). It is situated in the northern part of the National Park Northern Limestone Alps, Upper-Austria (47°50'30" N, 14°26'30" E). Mean annual temperature in the area is about 7 °C. January is the coldest month with an average temperature of –1 °C at 900 m a.s.l. and August is the warmest with 15.5 °C. Annual precipitation ranges from 1500 to 1800 mm. Snowfall occurs between October and May with continuous snow cover of about 4 months. Topographically, the monitoring site comprises a plateau (850–956 m a.s.l.) and a steep north facing slope (30–60°) extending from 850 m down to 550 m a.s.l. Triassic dolomite is the predominant bedrock material, partly interspersed with limestone plate layers. Soils are mainly chromic cambisols (“Kalksteinbraunlehm”) or hydromorphic stagnosols (pseudogley) on the plateau and lithic or rendzic leptosols (rendsina) with patches of chromic cambisols on the slope (Food and Agriculture Organization of the United Nations 2006). The potential natural vegetation of the plateau, beech-fir mixed forest, has largely been replaced by Norway spruce, *Picea abies* (L.) Karst., after the mixed forest was clear-cut at the beginning of the 20th century. The forest on the slope is a near-natural mixed beech (*Fagus sylvatica* L.) forest with ash (*Fraxinus excelsior* L.), maple (*Acer pseudoplatanus* L.) and spruce [*Picea abies* (L.) Karst.] as the most frequent additional tree species. Since the establishment of the monitoring site at Zöbelboden in 1992 management has been restricted to the removal of bark beetle infested trees.

Data collection

Data on tree recruitment were collected in two subareas of the Zöbelboden, which are equipped by a number of different field measurement devices (so called intensive measurement plots, about 0.5 ha in size), namely IP1 on the plateau and IP2 on the slope. The subareas were further divided into 31 (IP1) and 32 (IP2) 5 × 5 m areas. Within each of these areas, two 0.5 × 0.5 m plots were randomly selected and permanently marked by metal poles in 1993. Of the 126 plots, only the data for 49 of the IP1 and 57 of the IP2 plots

were included in the analyses. The data for the remaining 20 plots were excluded because of a windthrow event in the year 2006.

Vegetation and tree recruitment data

Vegetation on the plots was first recorded in August 2004 and was re-recorded, using the same method, in August 2007. For each plot, the percentage ground cover of every vascular plant and the total cover per plot were determined.

For tree seedlings and saplings the height and length of the terminal shoot increment in 2006 and 2007 were also measured. In addition, the age of each sapling was estimated by counting terminal bud scars and the occurrence of browsing damage noted by means of a yes/no scheme.

From these data for each plot, the species-specific tree recruitment rate was defined as the number of 1–5 years old seedlings and saplings recorded in 2007 (Appendix 1). Growth rates were defined as the mean terminal shoot increment in the years 2006 and 2007 for all seedlings and saplings < 10 years old.

Soil variables

Soil samples were collected in August and May 2007. The three subsamples collected 0.5 m apart at each of the four corners of each 5 × 5 m area were pooled. The August subsamples were shifted 0.25 m anticlockwise from where the samples were collected in May. Litter was removed and 5 × 5 × 5 cm soil cores from the mineral topsoil were collected. After sieving (2 mm, 5 mm), the soil was kept cool until chemical analysis in the laboratory of the Department of Chemical Ecology and Ecosystem Research at the University of Vienna.

In the laboratory, ammonium (NH_4^+) and nitrate (NO_3^-) contents, C:N ratios and pH for the May and August samples were measured (Appendix 2). Gross N mineralization and net N mineralization, respectively, were quantified for the August samples only. Nitrate was measured in CaSO_4 extracts (10 mM) using ion-chromatography (HPLC, Dionex, Vienna, Austria) and conductivity detection after chemical suppression (ASRS ultra, Dionex) using an anion exchange column (AS11, 250 mm × 4 mm, Dionex). Ammonium content was determined in KCl-extracts (1 M) by photometric analysis (Tecan-i-Control, Infinite M200) after oxidation by sodium dichloroisocyanure acid (Kandeler & Gerber 1988).

The ratio of organic carbon to nitrogen in bulked samples of soil (C:N ratio) was determined by elemental analyzer isotope ratio mass spectrometry (EA-IRMS, DeltaPLUS, Thermo Finnigan, Bremen, Germany). Samples were pretreated with 37% hydrochloric acid in order to fumigate inorganic C (carbonate) from the soil.

The pH-values of CaSO_4^- extracts were measured. Gross N mineralization rates were determined by using the pool dilution technique (Myrold & Tiedje 1986): 500 μl of $^{15}\text{NH}_4\text{Cl}$ (0.25 mM, 10 atom% ^{15}N) were applied to 2 × 2 subsamples (2 g) of fresh soil. Samples were subsequently incubated for 4 h and 24 h (incubation temperature 15 °C) and extracted with 2 M KCl. Ammonium in the extracts was diffused to acid traps and the ratio of $^{14}\text{N}:^{15}\text{N}$ was finally analysed by continuous-flow isotope ratio mass spectrometry (IRMS) using an elemental analyser coupled with a gas IRMS system (DeltaPLUS,

Finnigan MAT, Bremen, Germany). Rates of gross and net N mineralization respectively were calculated using the following equations:

$$(1) \quad m = ([\text{NH}_4^+]_t - [\text{NH}_4^+]_0) / t * ((\ln(\text{APE}_0 / \text{APE}_t) / \ln([\text{NH}_4^+]_t / [\text{NH}_4^+]_0))$$

where m is the gross N mineralization, $[\text{NH}_4^+]_t$ is the ammonium pool after 24 hours, $[\text{NH}_4^+]_0$ is the ammonium pool after 4 hours, APE (atom percent excess) is at $\%^{15}\text{N}_{\text{sample}} - \text{at}\%^{15}\text{N}_{\text{natural abundance}}$, t is the difference in incubation time between the subsamples (20 hours);

$$(2) \quad n = ([\text{NH}_4^+]_t - [\text{NH}_4^+]_0) / t$$

where n is the net N mineralization, $[\text{NH}_4^+]_t$ is the NH_4^+ -N pool after 24 hours, $[\text{NH}_4^+]_0$ is the NH_4^+ -N pool after 4 hours, t is the difference in incubation time (20 hours).

All the soil variables measured were spatially interpolated from the sampling points using inverse distance weighting (Philip & Watson 1982, Watson & Philip 1985). For this purpose, both subareas were subdivided into a 1×1 m grid and the soil variables were interpolated for each cell using a linearly weighted combination of all sampling points within each subarea. Then each plot monitored was assigned the interpolated value of the 1×1 m grid cell it was situated in. The mean of the August and May values were used for all further analyses. It has to be mentioned that owing to high small scale variation leading to weak spatial dependencies of the soil parameters more sophisticated geostatistical approaches were not applicable. Consequently, the expectation is that the interpolated data will be reasonable noisy.

Light conditions and microrelief

To quantify light conditions on the forest floor hemispherical photographs were taken during cloudy conditions at a height of one metre above each plot using a Nikon Coolpix 950 camera and a fisheye objective (Nikkor 14 mm) with a gimbal. At IP1 all photographs were taken on 10 August 2004 and at IP2 on 8 August 2007. Canopy openness (%) and total below canopy radiation ($\text{W}\cdot\text{m}^{-2}$) were determined using Gap Light Analyzer version 2.0 (GLA 2.0, Simon Fraser University British Columbia).

Micro relief properties were measured for each plot using an iron rod. The rod was laid across the plot both diagonally and across the middle. The distance from the rod to the surface was measured in the centre and 20 cm outside the plot margins in each direction. Distances measured outside the plot were then subtracted from the one in the centre and these differences were averaged. A positive value of this index suggests a convex and a negative one a concave surface.

Seed input

Estimates of seed input into each 0.5×0.5 m plot were calculated based on maps of all potential source trees on and within a radius of 20 m around the two IPs. For *Fagus sylvatica* and *Picea abies* the formula of Ribbens et al. (1994), corresponding to a Weibull dispersal kernel was used, with parameter values empirically calibrated by Kutter & Gratzner (2006) in a nearby mixed mountain forest.

For *Acer pseudoplatanus* and *Fraxinus excelsior* the respective parameter values were not available and so the mechanistically based WALD kernel (Katul et al. 2005) for wind dispersal of seeds was used instead, assuming a horizontal wind speed above the vegetation of $10 \text{ m}\cdot\text{s}^{-1}$ and a logarithmic wind profile within the forest stand (Nathan et al. 2001). Values of the necessary constants were taken from Skarpaas & Shea (2007) and Thompson & Katul (2008). Terminal velocities of the seeds were extracted from the LEDA functional traits data base (www.leda-traitbase.org). Release height was fixed at 80% of the height of the respective source tree. For each plot the probabilities that a seed released from each potential source tree would end up in the respective plot were cumulated. Hence this measure is not an estimate of the number of seeds landing in each plot, but a relative index of seed input probability.

Ellenberg indicator values

Averages of Ellenberg indicator values for light (L), acidity (R) and nutrient availability (N) were calculated for each $0.5 \times 0.5 \text{ m}$ plot as the unweighted arithmetic mean of the indicator values of all vascular plants recorded in the respective plot. Species with indifferent indicator values were excluded from these calculations.

Statistical analysis

The analysis focused on determining the effect of nitrogen availability on the recruitment and seedling/sapling growth of the four most abundant species of tree in the system studied, namely beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), maple (*Acer pseudoplatanus*) and spruce (*Picea abies*). Because of the blocked sampling design, mixed effects models were used to evaluate these relationships. All models were fitted for each species separately (except *Picea abies*, which was too rare on the plots) and, additionally, for the pooled data of all species. In each case, the analysis started with a basic model (bV) that included radiation input and soil pH, together with seed input in the case of recruitment. Then, in turn, each soil nitrogen variable (NH_4^+ , NO_3^- , C:N ratio, gross N and net N mineralization) was added to these basic models and their coefficients evaluated by means of z-tests. The same approach was adopted for the Ellenberg indicator values: basic models (bE) included L and R values, together with seed input in the case of recruitment, and N-values were then added to the models. Finally, the nine models (bV and bE + five models with one of the measured nitrogen variables added to bV + one model with Ellenberg's N added to bE) were compared per response and species (or pooled species, respectively) by means of Akaike weights. Akaike weights scale differences in the models' Akaike information criterion (AIC) between 0 and 1 and, in doing so, indicate the probability that a particular model is the best description of a given dataset among, in this case, the nine candidate models (Burnham & Anderson 2002, 2004).

In the case of recruitment (= number of seedlings per plot), analyses were performed by means of generalized linear mixed effects models (GLMMs) applying the canonical log-link for Poisson distributed data. For growth (= shoot length increment per individual seedling) Gaussian LMMs were used after a Box-Cox-transformation of the response variable to achieve a near-normal distribution, if necessary. In both cases, the $5 \times 5 \text{ m}$ fields, that both of the subareas were divided into, were defined as the relevant grouping structure and random intercepts estimated for each group. More complex model structures

with random effects for each predictor in the model, or with interactions among the predictor variables, did not converge using the available optimization algorithms.

All predictor variables were standardized to mean zero and unit variance before fitting the models. GLMMs were performed by means of the *glmer* function in the R-package lme4 (Bates et al. 2008), LMMs by means of the *lme* function in the package nlme (Pinheiro et al. 2008).

Results

Correlation of measured variables and Ellenberg's indicator values

There was a strong positive correlation between pH and Ellenberg's R value, and between gross N mineralization, ammonium concentration and Ellenberg's N (Fig. 1, $R^2 = 0.32\text{--}0.54$). C:N ratio, nitrate concentration and net N mineralization were less closely linked to Ellenberg's N ($R^2 < 0.2$ throughout). In contrast to gross N mineralization and ammonium concentration, net N mineralization and nitrate concentration were negatively correlated to the Ellenberg N indicator value. There was no correlation between light availability at the forest floor and Ellenberg's L-values.

Recruitment

In total there were 205 seedlings/saplings (< 5 years old) of *Acer pseudoplatanus*, 95 of *Fraxinus excelsior*, 44 of *Fagus sylvatica* and 12 of *Picea abies* in 106 plots sampled (Appendix 1). Focusing on the pooled data for all four species revealed a general decrease in tree recruitment in the more acidic plots and an increase with increase in light levels, whereas calculated seed input was not significantly correlated to seedling numbers per plot (Table 1). In the single species models, however, an effect of the input of solar radiation was not detectable and soil pH only affected beech recruitment.

For all four species, seedling numbers increased with rising C:N ratios and decreased with rising NO_3^- contents. None of the other three N variables were correlated with tree recruitment. Models for individual species revealed that these general trends mask the opposing relationships to the nitrogen gradient shown by *F. sylvatica* and *A. pseudo-platanus*: the number of maple seedlings decreased and beech seedlings increased with nitrate content; and vice versa, maple seedlings became more frequent with rising C:N ratios (i.e. lower nitrogen content), whereas beech seedlings became rarer (although not significantly so).

Despite the rather close correlation between pH and Ellenberg's R, the effect of soil acidity on both *F. sylvatica* and pooled seedling numbers was not detectable when the Ellenberg indicator values were used as predictors in this model. Instead, R was significantly negatively correlated with the number of maple seedlings per plot, an effect which was not recorded when the analysis was based on the variables measured. In contrast, Ellenberg's N was related to the recruitment patterns of *F. sylvatica* and *A. pseudo-platanus*, as in the models using the measured variables. However, instead of opposing trends, the recruitment of both species was negatively related to Ellenberg's nitrogen indicator value.

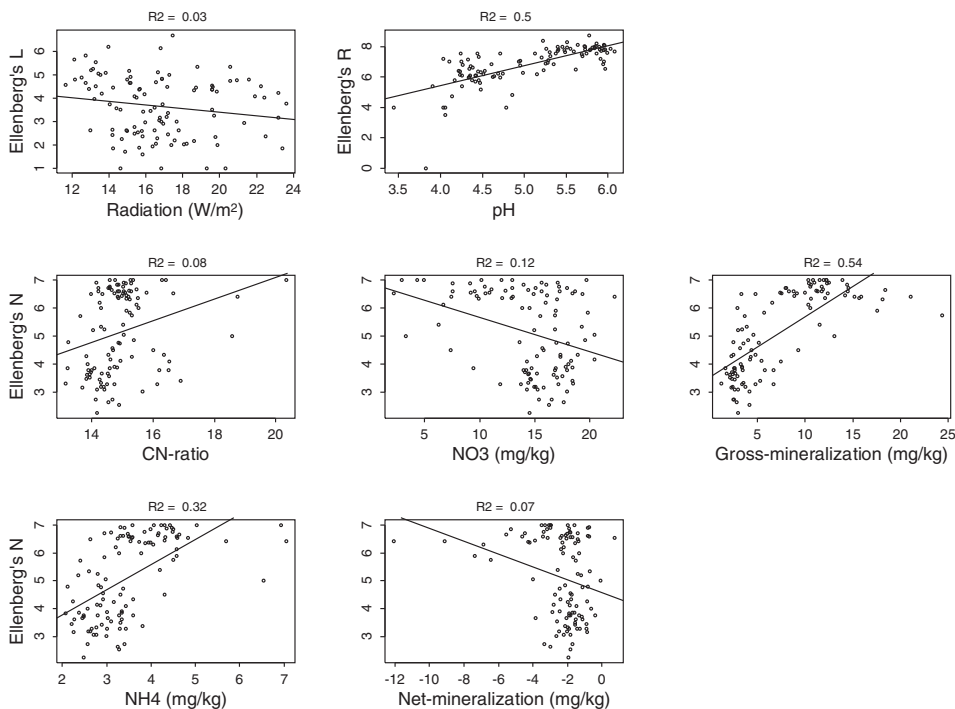


Fig. 1. – Correlations between unweighted averages of Ellenberg's indicator values L, R and N and incoming radiation, soil pH and soil nitrogen recorded for 106, 50 × 50 cm plots in a montane forest in the North-eastern Calcareous Alps in Austria. R² values represent the squares of Pearson's correlation coefficients. The lines are least-squares regression fits.

Table 1. – Coefficients of predictor variables in generalized linear mixed effects models relating the number of tree seedlings recorded in 50 × 50 cm plots in a mixed montane forest in the North-eastern Calcareous Alps to various predictor variables. In the left section of the table are the results of models with incoming radiation and soil chemical conditions as predictors and in the right section results of models with Ellenberg indicator values as predictors. * P < 0.05, ** P < 0.01, *** P < 0.001. Gross (min) and net (min) are gross and net mineralization rates respectively. L, R, and N are the Ellenberg indicator values for light, soil reaction and nitrogen supply.

	Variables measured				Ellenberg values				
	<i>Acer</i>	<i>Fagus</i>	<i>Fraxinus</i>	All	<i>Acer</i>	<i>Fagus</i>	<i>Fraxinus</i>	All	
Seeds	-0.02	0.11	-0.10	0.00	Seeds	-0.01	0.06	-0.06	-0.05
Radiation	0.06	0.42	0.00	0.10*	L	0.16	0.24	0.09	-0.11
pH	-0.03	0.64*	0.08	-0.28*	R	-0.27**	0.75	-0.15	-0.08
C:N ratio	0.18**	-0.11	0.03	0.23***	N	-0.21*	-0.55*	0.01	-0.08
NO ₃	-0.18*	0.84*	-0.08	-0.17*					
Gross (min)	0.04	-0.79	0.05	0.13					
NH ₄	0.11	-0.60	-0.20	0.02					
Net (min)	-0.06	-0.16	-0.04	-0.08					

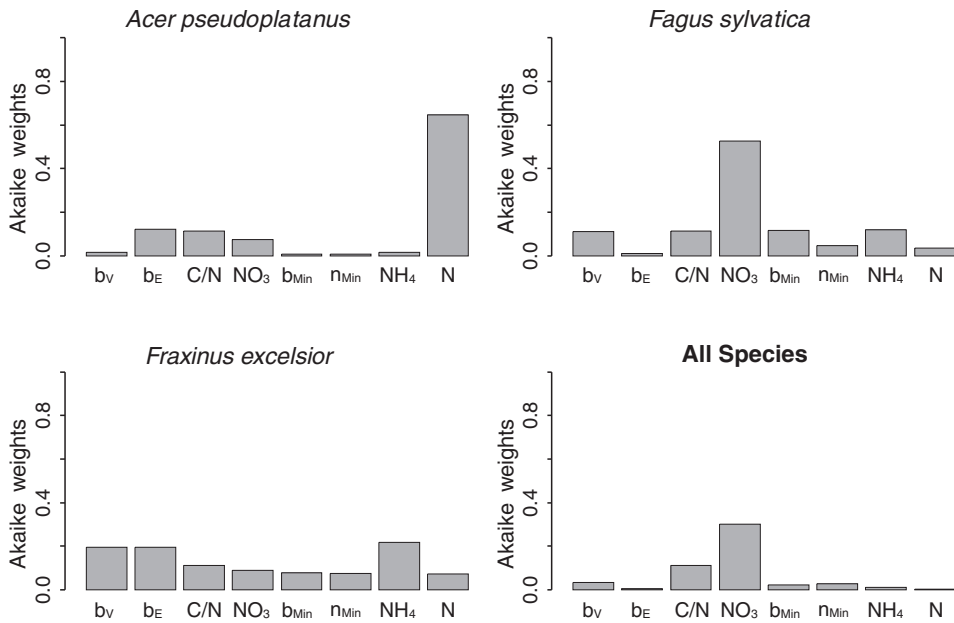


Fig. 2. – Akaike weights for generalized linear mixed effects models relating the number of tree seedlings recorded in 50 × 50 cm plots in a mixed montane forest in the North-eastern Calcareous Alps to various predictor variables. b_V and b_E are models with predictor variables soil pH and incoming radiation, or Ellenberg’s L and R values, respectively. The other models were b_V and b_E models that included also one of the soil variables (C:N ratio, NO₃ content, b_{Min} = gross mineralization, n_{Min} = net mineralization or NH₄ content) or Ellenberg’s N.

Comparing all nine candidate models by means of Akaike weights demonstrates that models using NO₃⁻ contents as a measure of nitrogen availability provide the best descriptions of the beech and pooled dataset, whereas maple seedling distribution is best described using an ‘Ellenberg model’ that includes N (Fig. 2). Recruitment of ash was not significantly correlated with any of the predictor variables used (Table 1) and hence Akaike weights hardly differed among candidate models.

Growth

A total of 243 individuals of *Acer pseudoplatanus*, 89 of *Fraxinus excelsior*, 71 of *Fagus sylvatica* and 12 of *Picea abies* were included in the analysis of growth patterns (Appendix 1). Information on trees with browsing damage was not considered in the statistical analyses.

Similar to recruitment, the growth of seedlings of all four species was lower at the lower pH values, whereas no effect of the level of solar radiation on shoot growth was detected (Table 2). In the single species models, a relationship between growth and pH was only detectable (marginally non significant, i.e. 0.1 > P > 0.05) in the case of *A. pseudoplatanus*.

Recruitment and growth models were also consistent in terms of the species that correlated with the nitrogen gradient: again, maple and beech responded to the nitrogen variables measured, whereas ash did not. However, both in terms of the nature of these relationships and the relevant measures of N availability, growth models differed from those of

Table 2. – Coefficients of predictor variables in linear mixed effects models relating the shoot growth of tree seedlings recorded in 50 × 50 cm plots in a mixed montane forest in the North-eastern Calcareous Alps to various predictor variables. In the left section of the table are the results for models with incoming radiation and soil chemical conditions as predictors and in the right section the results of models with Ellenberg indicator values as predictors. * P < 0.05, ** P < 0.01, *** P < 0.001. Gross(min) and Net(min) are gross and net mineralization rates respectively. L, R, and N are the Ellenberg indicator values for light, soil reaction and nitrogen supply.

	Variables measured				Ellenberg values				
	<i>Acer</i>	<i>Fagus</i>	<i>Fraxinus</i>	All	<i>Acer</i>	<i>Fagus</i>	<i>Fraxinus</i>	All	
Radiation	0.04	0.03	-0.08	-0.02	L	0.03	-0.11	0.01	0.02
pH	-0.13	-0.09	0.02	-0.10*	R	-0.13	-0.01	0.06	-0.09
C:N ratio	-0.12	0.00	-0.17	-0.15*					
NO ₃	0.09	0.00	0.05	0.06					
Gross(min)	0.24*	0.14*	0.02	0.22*	N	0.10	0.07	0.04	0.10*
NH ₄	0.24*	0.18**	-0.07	0.16*					
Net(min)	-0.11	-0.07	-0.07	-0.08					

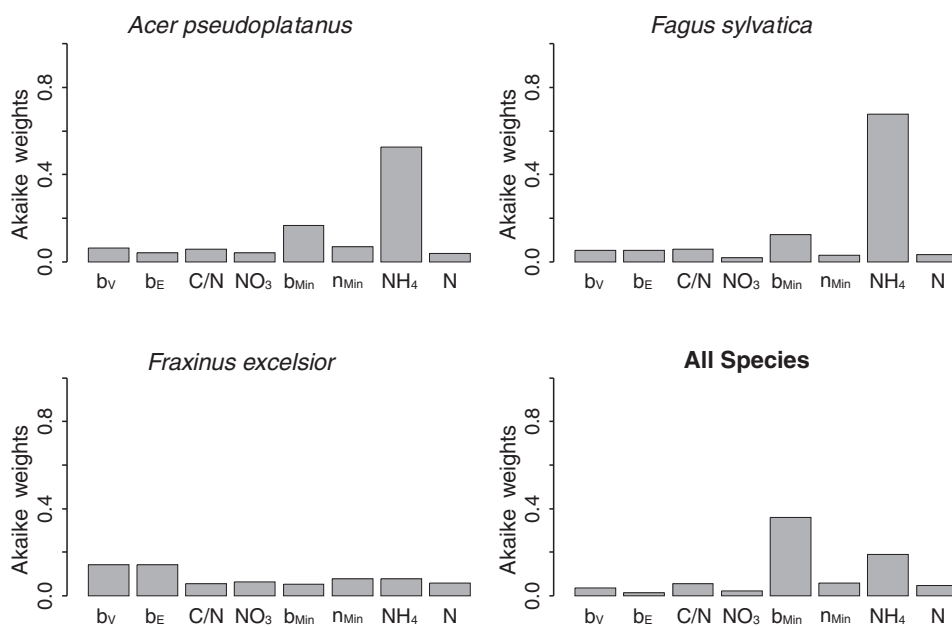


Fig. 3. – Akaike weights for linear mixed effects models relating shoot growth of tree seedlings recorded in 50 × 50 cm plots in a mixed montane forest in the North-eastern Calcareous Alps to various predictor variables. b_V and b_E are models with predictor variables soil pH and incoming radiation, or Ellenberg's L and R values, respectively. The other models were b_V and b_E models that included also one of the soil variables (C:N ratio, NO₃ content, b_{Min} = gross mineralization, n_{Min} = net mineralization or NH₄ content) or Ellenberg's.

recruitment. In particular, a high nitrogen content generally enhanced growth and the most relevant measures were NH₄⁺ concentrations and gross mineralization rates (Table 2, Fig. 3). In contrast, nitrate concentrations, and net mineralization rates, were not correlated

with either the pooled growth or that of any of the species. C:N ratios were at least significant in the model of the data for all the species, with an effect consistent with those of NH_4^+ concentrations and gross mineralization rates: the lower the C:N ratio (i.e. the higher the N content), the higher the growth rates.

As in the case of recruitment, the rather close relationship between pH-values and R is not associated with a corresponding effect of R on tree seedling growth in the 'Ellenberg model' of the pooled data (Table 2), although the trends were at least consistent. With respect to N, the Ellenberg value was also clearly less sensitive than the measured variables. The growth of maple and beech was not significantly related to Ellenberg's N. Only for the pooled data of all four species of trees is the enhancing effect of nitrogen on tree seedling growth detectable.

The Akaike weights also indicated the superiority of measured variables over Ellenberg's indicator values for explaining seedling growth rates (Fig. 3). With the exception of ash, which did not respond to any (combination of) predictor variable(s), models using measured N variables (either NH_4^+ concentrations or gross mineralization rates) were always the ones most likely to provide the best explanation of the spatial growth patterns in the data.

Discussion

Correlation among measured variables and Ellenberg's indicator values

A close relationship between soil pH and the Ellenberg indicator value R (Fig. 1) is reported in previous studies (Ellenberg et al. 1992, Thimonier et al. 1994, Schaffers & Sýkora 2000, Diekmann 2003, Mellert & Bernhardt-Römermann 2005, Seidling & Fischer 2008) and the current results ($R^2 = 0.5$) are very similar to those of Ertsen et al. (1998, $R^2 = 0.54$) and Wamelink et al. (2002, $R^2 = 0.44$). Similarly, poor correlations between the N indicator value and either nitrate or total soil nitrogen content, or net nitrogen mineralization are documented elsewhere (Schaffers & Sýkora 2000, Diekmann 2003, Mellert & Bernhardt-Römermann 2005) and hence not surprising.

The concentration of ammonium was positively and nitrate negatively correlated with Ellenberg's N. One reason for the negative relationship of nitrate with Ellenberg's N may be that nitrate values above a certain level indicate an excess of N and therefore there is not a linear correlation with plant growth. Nitrate concentrations measured in this study ranged from 3 to 20 $\text{mg}\cdot\text{kg}^{-1}$ soil and thus covered a range from medium to very high values (Booth et al. 2005). The rather low positive correlation between the C:N ratio and Ellenberg's N may be due to the small variability recorded in soil C:N ratio in the study area (due to similar bed rock and vegetation characteristics).

There was no correlation between light intensity and Ellenberg's L. This result does not contradict the well-known relationship between light availability and tree recruitment, but is rather related to the low variance in radiation, which was monitored below the tree canopy in all the plots. However, it is possible that the hemispherical photographs did not capture the relevant differences in the light environment sufficiently accurately and that measurements of incoming direct radiation by means of PAR sensor would have delivered a significant correlation with Ellenberg's L values.

Gross N vs. net N mineralization

A novel outcome of this study is the combined, rather strong, positive correlation of Ellenberg's N with gross N mineralization and weak negative correlation with net N mineralization. Net N mineralization, which is defined as the difference between N mineralized by microbes (i.e. gross N mineralization) and that immobilized by microbes (i.e. gross N immobilization), is usually measured in the absence of plant N uptake. Thus, net N mineralization only reflects the amount of N that is potentially available for plants after meeting the needs of microbes. This represents, however, a rather unrealistic scenario as in a natural setting plants actively compete with microbes for N (Hodge et al. 2000). In a spatially structured environment, such as soil, gradients from N-rich micro sites (where microbial N mineralization is high) to more N-depleted micro sites (where microbial N immobilisation dominates) may develop (Schimel & Bennett 2004). It is likely, that plants benefit from N flows between such microsites. From this point of view, gross N mineralization, which describes the total NH_4 production by microbes, independent of whether it is taken up by microbes or by plants, may be a much better indicator of plant N availability than the more widely used net N mineralization. The strong relationship between gross N mineralization and Ellenberg's N and that gross N mineralization rates rather than other N variables are more closely associated with seedling growth rates, strongly support this concept and indicate that plants are good competitors for N. The results presented confirm those of Bengtson et al. (2006) that demonstrate a close relationship between gross N transformation rates and spatial variation in total abundance and species composition of the understorey vegetation.

Comparison of measured variables and indicator values for predicting vital rates of trees

Agreement among models fitted using Ellenberg's indicator values and the variables that were measured is poor. This may be partly due to the low correlations among some of the variables and Ellenberg's indicator values. However, even when correlations were high, results were not necessarily consistent. For example, the significant positive response of beech recruitment to pH was not indicated by models based on Ellenberg's R, and, vice versa, the response of maple recruitment to R is not paralleled in the models using measured variables as predictors. The contradiction between a close correlation among Ellenberg values and measured variables on the one hand and a differential response of species to these two measures of environmental gradients on the other hand is especially salient for the positive effect of gross mineralization on seedling growth rates of *Fagus* and *Acer*. Moreover, in the detailed single-species analysis N did not appear to have a growth-enhancing effect at all, or have the opposite effect to nitrate content and C: N ratios on maple and beech recruitment. With respect to nitrogen in particular, the low correlation between Ellenberg's N and measured variables may be because the indicator represents the simultaneous effect of a couple of interacting soil variables (Schaffers & Sýkora 2000, Diekmann 2003, Wagner et al. 2007). For example, Smart et al. (2010) calibrated mean Ellenberg indicator value N against percentage soil moisture content, pH, organic carbon (%) and organic nitrogen (%) and found that mean Ellenberg's N was best predicted by a combination of these four soil variables.

Overall, the results indicate that the variables measured are more likely to result in significant correlations between gradients in soil nitrogen content and tree seedling or sapling

performance than Ellenberg's indicator values. The decreased sensitivity of the indicator values recorded in this study might in part be a consequence of the small size of the plots (Diekmann & Falkengren-Grerup 1998, Gégout & Křížová 2003, Mellert & Bernhardt-Römermann 2005, Wamelink et al. 2005). In small plots, stochastic effects on species composition may override the effects of environmental conditions. On the other hand, soil attributes may vary at very fine scales in calcareous mountain forests, and hence the species composition even of a 0.5×0.5 m plot may obscure possible small-scale differences among the sites of individual tree saplings. In this context, it is very likely that the variation recorded in this study is due to the spatial interpolation of the soil variables measured at points separated by 5 m.

Effects of nitrogen on tree sapling performance

The recruitment of maple and beech was correlated with different soil nitrogen variables: although both species were obviously affected by nitrogen availability, the C:N ratio had a highly significant effect on the number of seedlings of maple, but not of beech. With respect to growth, sensitivities to the various soil nitrogen indicators were more consistent among species with both maple and beech responding similarly to nitrogen gradients.

The only species that was obviously insensitive to N, whether measured directly or by means of Ellenberg indicator values, was *F. excelsior*. This is only partly consistent with the findings of other studies. Although Weber-Blaschke et al. (2008), for example, also found a positive relationships between foliar N and growth of maple, but not of ash, these authors nevertheless suggest that ash requires soils with a high microbial activity and availability of N and P, and a high base saturation (Hofmeister et al. 2004). However, as shown by Hofmeister et al. (2004) the distribution of ash is not necessarily affected by high availability of N, but mainly by light availability and competitive interactions. In general, tree regeneration in mature temperate forests usually depends on a complex of interacting environmental factors including light intensity, water supply, bedrock material and soil nutrient supply other than N, and biotic and abiotic disturbance regimes (Hulme 1996, Leuschner & Rode 1999, Nagamatsu et al. 2002, Kupferschmid & Bugmann 2005, Baier et al. 2007) and it may well be that the predominant role of these variables supersedes any effect that nitrogen has on the regeneration of certain tree species over the limited ranges of these variables recorded in a given study system.

Vital rates

In general, recruitment and growth of both maple and beech respond to the availability of nitrogen. However, growth and recruitment of one species did not necessarily respond to the same indicator of nitrogen availability: whereas seedling numbers were affected by nitrate content and C: N ratios, growth responded to gross mineralization rates and ammonium. The independence of the growth rates of *Acer pseudoplatanus* of C: N ratios indicated by this study accords with the results published by Jensen et al. (2008) and similar results for two other species of maple (Finzi et al. 1998). Moreover, different vital rates of the same species might even show opposite relationships with the nitrogen gradient: whereas maple growth was enhanced where there was a greater availability of nitrogen, recruitment was greater where there was a low N content. These findings agree with the idea that the abiotic niches of plants may change during their life cycle and that different vital rates may respond differently to environmental gradients (Nakashizuka 2001, Beckage & Clark 2003).

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Souhrn

Na monitorovacích plochách v Zöbelboden v severních Alpách v Rakousku byl studován vliv znečištění ovzduší na lesní ekosystémy. Studie sledovala, jak jsou časná stádia *Picea abies*, *Fagus sylvatica*, *Fraxinus excelsior* and *Acer pseudoplatanus* ovlivněna dostupností dusíku; proměnné byly přímo měřeny nebo vyjádřeny pomocí Ellenbergových indikačních hodnot. Na 106 plochách o velikosti 0,5 × 0,5 m byla měřena hodnota pH, obsah NH₄⁺, NO₃⁻, mineralizace a poměr C:N ve svrchní vrstvě půdy. Vzházení semen a růst semenáčů byl vztahován jednak k těmto přímo naměřeným proměnným, a jednak k průměrným Ellenbergovým hodnotám, vypočítaným na základě druhového složení ploch; data byla analyzována pomocí lineárních nebo generalizovaných lineárních smíšených modelů. Přímá měření vysvětlovala růst stromů lépe než Ellenbergovy indikační hodnoty. Jak obsah NH₄, tak rychlá celková mineralizace sice podporovaly růst *Fagus sylvatica* and *Acer pseudoplatanus*, lišily se však ve vlivu na vzházení těchto druhů. Vzházení a růst *Fraxinus excelsior* nebyly ovlivněny žádnou ze studovaných proměnných. Mezidruhové rozdíly ve využívání zdrojů dusíku a rychlosti jeho přísunu tak mohou přispívat ke koexistenci druhů stromů ve smíšeném horském lese.

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Appendix 1. – Maximum, minimum, mean values and standard deviation (SD) of the response variables of (A) recruitment (= the number of 1–5 year old seedlings and saplings recorded in 2007); or (B) growth (= the mean terminal shoot increment in cm in 2006 and 2007) of seedlings and saplings of *Acer pseudoplatanus*, *Fraxinus excelsior*, *Fagus sylvatica* and *Picea abies*; n is the number of plots in which recruitment was recorded (with the number of individuals in brackets) or the number of individuals for the growth measurements.

A. Recruitment	n	Max	Min	Mean	SD
<i>Fagus sylvatica</i>	106 (44)	7	0	0.4	1.1
<i>Acer pseudoplatanus</i>	106 (205)	10	0	1.9	1.8
<i>Fraxinus excelsior</i>	106 (95)	6	0	0.9	1.1
<i>Picea abies</i>	106 (12)	1	0	0.1	0.3
B. Growth					
<i>Fagus sylvatica</i>	71	5	0.2	1.5	1.0
<i>Acer pseudoplatanus</i>	243	11.5	0.2	2.2	1.8
<i>Fraxinus excelsior</i>	89	8	0.3	2.1	1.3
<i>Picea abies</i>	12	1.8	0.8	1.4	0.3

Appendix 2. – (A) Maximum, minimum, mean values and standard deviation of measured environmental variables; Radiation [$\text{W}\cdot\text{m}^{-2}$] was measured during cloudy conditions at a height of one metre above each plot. C:N ratio, NO_3^- [$\text{mg}\cdot\text{kg}^{-1}$], NH_4^+ [$\text{mg}\cdot\text{kg}^{-1}$] and pH are averages for two measurements (May and August 2007). Samples for Gross(min) and Net(min) [$\text{mg}\cdot\text{kg}^{-1}$] refer to measurements for August 2007. The samples consisting of three subsamples taken at the corners of each 5×5 m area were pooled. Litter was removed and $5 \times 5 \times 5$ cm soil cores from the mineral topsoil were taken. Measurements were spatially extrapolated for each plot by inverse distance weighting. (B) Maximum, minimum, mean values and standard deviation of Ellenberg indicator values. Unweighted averages of Ellenberg indicator values were calculated using the arithmetic mean of indicator values per plot. Therefore the percentage cover of each species in a plot was transformed to presence/absence data. Indifferent indicator values were not included in the analyses; n is the number of soil samples used for chemical analyses (with the total number of soil samples in brackets when there were two measurements) and the number of radiation measurements (A) and the number of plots used for calculations of Ellenberg indicator values (B).

A. Measured variables	n	Max	Min	Mean	SD
pH	91 (182)	6.1	3.4	5.0	0.7
Radiation	106	23.6	11.6	16.8	2.8
C:N ratio	91(182)	20.3	13.1	14.9	1.0
Gross(min)	91	24.4	1.3	8.0	5.3
Net(min)	91	0.7	-12.1	-2.7	2.2
NH_4^+	91(182)	7.0	2.1	3.6	1.0
NO_3^-	91(182)	22.2	2.2	14.5	4.0
B. Ellenberg indicator values					
R	106	8.7	0	6.8	1.3
L	106	6.7	1.0	3.7	1.3
N	106	7.0	2.3	5.1	1.5