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ORIGINAL PAPER

Soil N mineralization profiles of co-existing woody vegetation islands at the alpine tree line

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Abstract Tree lines form a transition ecotone from forest to tundra both at high elevation and high latitude and occur in a number of different forms. Nitrogen (N) deficiency is considered to be a factor involved in tree line formation, and also N dynamics are considered to differ between the trees and the ericaceous vegetation of the tundra. In the Austrian Alps at the tree line, N availability and N mineralization in soils of different vegetation types (*Picea abies*, *Pinus mugo* and *Rhododendron ferrugineum*) as well as total phenols were determined. Soil from under *P. abies* was taken from two different tree line forms, an island type and a diffuse type, as well as from *P. abies* growing at a lower elevation. N mineralization was measured in situ using a covered PVC tube incubation method and in a laboratory incubation under controlled conditions. Ion exchange resin capsules were installed at the interface of humus and mineral soil for estimating N in the soil solution. Net N mineralization showed a similar pattern for the vegetation types for both the in situ and laboratory incubation. The soil humus layer had the highest levels of N mineralization compared to the other soil layers. N mineralization rates were similar in *P. abies* and *P. mugo* at the tree line regardless of tree line form. Rates of N mineralization were lower under *R. ferrugineum* than the tree species, but this lower rate was not related to the occurrence of high levels of total phenols in the soil. Nitrogen deficiency was not evident in the island-type tree line, but was evident in the diffuse tree line type.

Keywords Tree line · Soil N mineralization · In situ field incubation · Soil N availability · Resin capsule · Woody vegetation islands

Introduction

Tree lines form a transition ecotone from forest to tundra both at high elevation and high latitude (Harsch and Bader 2011). In mountains, tree lines are delimited at the upper elevation by the limit of tree species occurring in any form and at the lower elevation by the start of continuous forest > 3 m in height (Harsch and Bader 2011; Holtmeier and Broll 2005). Harsch and Bader (2011) define four types of tree line (a) diffuse, (b) abrupt, (c) island and (d) krummholz. The diffuse trees line form is characterized as having a gradual transition from trees > 3 m in height to alpine vegetation, whereas the island tree line form is characterized by small islands of either trees > 3 m or trees with stunted krummholz growth forms. In mountain ecosystems in particular, the vegetation at and above the tree line is considered to be highly vulnerable to changes in

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climate, pollutants and nutrient inputs (Balestrini et al. 2013). Particularly diffuse and abrupt tree lines are advancing (Harsch and Bader 2011) with the potential driving factors being an increase in temperature, in atmospheric carbon (C) dioxide and in deposition of N (Grace et al. 2002; Stevens and Fox 1991). The ecology and distribution of tree lines have been studied for more than a century, and limitation of growth has been suggested to be due to a number of causes (Jobbagy and Jackson 2000; Stevens and Fox 1991). Traditionally growth limitation has been suggested to be due to limitation of C caused by lower photosynthesis at low temperatures and a short growing season (Harsch and Bader 2011; Körner 1998; Wardle 1993). However, studies of gas exchange and non-structural carbohydrates have shown no evidence for C limitation (Körner 1998). Studies conducted at high latitude tree lines in Alaska show that N and phosphorus (P) availability is generally low in Alaskan spruce forest, and release of N and P from dead organic matter is slow due to temperature-limited decomposition (Schulze et al. 1994). Nitrogen limitation has been suggested to be a major factor restricting plant growth at the tree line, both at high latitude tree lines (Chapin et al. 1995; Sullivan et al. 2015) and alpine high elevations tree lines (Dawes et al. 2017; Thébault et al. 2014). Although nutrient availability can be relatively low at the tree line due to low microbial mineralization and N fixation rates at low temperature (Loomis et al. 2006), the concept that tree line stands have a greater degree of nutrient limitation than forested stands has also been challenged (Loomis et al. 2006). Körner (2012) has suggested that low nutrient availability is not main factor determining tree line position at a global scale.

Species such as *R. ferrugineum*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* are the dominant ericaceous plant species at the Alpine tree line on siliceous bedrock, and often growing in discrete patches. A characteristic of ericaceous plants is that they have litter with low amounts of N and P (Cornelissen et al. 2001). A function attributed to ericoid mycorrhizas is the ability to mobilize N and P from low-quality litter substrates using extracellular enzymes (Read et al. 2004). Wurzburger and Hendrick (2007) suggested that *Rhododendron maximum* litter alters N cycling through the formation of recalcitrant polyphenol–organic N complexes. Read et al. (2004) and DeLuca et al. (2002) showed that in forests ericaceous understories often result in lower N mineralization and decomposition rates.

The concentration of N in soils is controlled by net mineralization, leaching losses and uptake by plants and microorganisms (Khanna and Raison 2013). The degradation of organic matter through N mineralization results in the sequential production of ammonium and nitrate. The main factors controlling ammonification and nitrification in forested ecosystems are moisture, temperature and substrate quality (Gadgil and Gadgil 1978), and there is, however, uncertainty about the relative importance of each of these factors. Zak et al. (1999) showed that net N mineralization significantly increased with temperature; however, Nadelhoffer et al. (1991) indicated that the quality of organic matter was more important than temperature in controlling N- and C-mineralization rates in tundra plant communities. In other studies, N mineralization was significantly correlated with litter quality measured as the (lignin + polyphenol)/N ratio (Kladivko and Keeney 1987). Some researchers also pointed out that mineralization of soil N depends on a wide range of factors, such as the C/N ratio (Frankenberger and Abdelmagid 1985), the N content (Iritani and Arnold 1960; Zhao et al. 2016), lignin content (Abbasi et al. 2015; De Neve et al. 1994), or the light fraction organic matter of the soil (Janzen et al. 1992; Sierra 1996).

Measurements of the net N mineralization rate in forest soils generally aim at providing an index which can be correlated with nutrient cycling. There are several methods which can be used to determine soil net N mineralization, these included laboratory-based methods using incubation under standard (and usually optimum) conditions of temperature and moisture (Adams et al. 1989) or in situ methods using incubation under field conditions using ambient soil temperatures and moisture. All of the techniques involve prevention of N uptake by plants either through the removal of roots or cutting of roots, thus allowing N mineralized during incubation to accumulate. However, as N uptake by soil microbes is not eliminated, net N mineralization measures N released by mineralization minus N immobilized in the soil microbial biomass. The covered-cylinder method is the most commonly used in situ method. The cylinder is usually constructed from a PVC or metal pipe that is capped to exclude rainfall (Hanselman et al. 2004). Ion exchange resin-based techniques are used for measuring soil nutrient availability and leaching flux (DeLuca et al. 2002; Giese et al. 2011; MacKenzie et al. 2006; Johnson et al. 2005), but can also be used to provide quantitative estimates of both net NH_4^+–N and NO_3^-–N production (Hart and Firestone 1989).

In the present study, we tested the hypothesis that different vegetation species coexisting at the alpine tree line have different rates of N mineralization, and we assessed whether N limitation occurs at the alpine tree line. To this end, we utilized two tree line forms, islands of coexisting woody vegetation (*Picea abies*, *Pinus mugo*, *R. ferrugineum*) and a diffuse tree line of closed *P. abies*. This was compared to a lower elevation *P. abies* stand which allowed a comparison of a similar stand structure at different elevations.

Materials and methods

Site description

The study site is located in the Wasserberg area of the Stift Heiligenkreuz forest estate in the central Alps in Austria. The work was conducted at two types of tree line (tree islands and a diffuse tree line) and at a lower elevation in a closed forest. The forest area of the Wasserberg is dominated by *P. abies* L. Karst, as the potential natural vegetation. On June 8, 2015, at the tree islands, five replicate plots were established between 1668 and 1791 m above sea level on a southeast facing slope (47°19′N, 14°43′E). Each plot contained discrete areas dominated by *P. abies, P. mugo and R. ferrugineum*. The *R. ferrugineum* plots also had *V. myrtillus* growing within the more open bush parts. The plots were ca. 120 m apart. The *P. abies* trees were ca. 4 m in height and estimated to be ca. 30 years old and formed tree islands of on average of 5–8 trees. The tree islands are part of a natural encroachment of the tree line. On June 8th, 2016, five replicated plots were established in a diffuse tree line of *P. abies* at an elevation of 1800 m ca. 300–500 m from the island-type tree line. The trees were estimated to be 90–120 years old and tree heights are 6–9 m in height. The stand ends at ca. 50-m distance and 30-m elevation from the plots. At a lower elevation (1395 m above sea level), five replicated plots were established in a closed canopy area of the *P. abies* forest (47°18′559″N, 14°45′271″E) on June 8, 2015. The minimum distance between the plots was ca. 40 m. The trees were estimated to be between 90 and 120 years old, and ca. 40 m in height and had a mean diameter at breast height (DBH) of ca. 50 cm. Soils at the sites are developed from gneiss and are Dystric Cambisols with an H layer of ca. 6 cm and an A layer of ca. 10 cm.

Sampling and N mineralization analysis

Two soil cores were taken to a depth of 40 cm from each of the species subplots of *P. abies*, *P. mugo* and *R. ferrugineum* at tree islands site, at the *P. abies* site of lower elevation on June 8, 2015, and at the diffuse *P. abies* tree line on June 8, 2016, using a 7-cm-diameter stainless steel corer. Soil samples were directly returned to the laboratory, stored at 4 °C and analyzed within 24 h. All soil cores were divided into H, A, B horizons according to Guidelines for Soil Description 2006, FAO (FAO 2006), and the soil of the diffuse *P. abies* tree line had no B horizon within 40 cm. Five grams of fresh soil (sieved to $\leq$ 2 mm) taken from each horizon was extracted with 50 ml 2 M KCl, shaken for 2 h on a reciprocating shaker at a speed of 22 rotations per minute. The extracts were then left to stand for 10 min, filtered through Whatman 42 (pore size 2.5 µm) filter paper, before NH_4^+ and NO_3^- in the extracts were determined using a FIA5000 analyzer (the techniques are based on gas diffusion using a semipermeable membrane in combination with a pH indicator). Another 5 g of fresh soil was filled into 100-ml tubes which were then covered with Parafilm (Bemis Company Inc), allowing air exchange but retarding moisture loss, and were incubated in a growth chamber at 20 °C with a 24-h light/dark cycle for 30 days. Ammonium and NO_3^- were subsequently extracted from the soil and analyzed as described above. Net N mineralization was calculated from the difference between the initial values of NH_4^+ and NO_3^- at time zero and the values after 30-day incubation in the growth chamber.

To determine in situ N mineralization, two PVC (polyvinyl chloride) tubes covered by plastic bags were inserted to 15-cm-depth soil in each species subplot at each tree line plot on June 8, 2015. The PVC tubes were sharpened with a bevel on the outside at the base to minimize soil compaction in the core during installation. The incubation tubes were recovered on July 20, 2015. The soil in the PVC tubes was transported undisturbed to the laboratory. The soil was then extracted from the tubes, sieved to $\leq$ 2 mm, and on 5 g fresh soil NH_4^+ and NO_3^- were determined as described above.

To determine availability of NH_4^+ and NO_3^-, two ion exchange resin capsules (PST-2; Unibest) were installed at the interface of the humus and mineral soil for estimating soil N availability in each species at each plot on June 8, 2015. The resin bags consisted of 25 g anion and cation exchange resin beads in a nylon mesh capsule. The resin capsules were recovered on July 20, 2015. The resin capsules were returned to the laboratory, and adhering soil particles were carefully removed with Milli-Q water. The resin capsules were extracted with 2N HCl and shaken on an over-end reciprocating shaker for 30 min. The solution was removed and the procedure was repeated another two times, giving a total of three washes and a single 60-ml extraction volume. The extracts were neutralized with 60 ml 2N KOH, and NH_4^+ and NO_3^- in the extracts were determined using a FIA5000 analyzer.

Soil pH, total C, total N analysis

Soil pH was determined in the laboratory on field moist soil in a 1:3 soil/distilled water slurry using a pH meter (Schott). For analysis of total C and total N, soil dried at 60 °C was finely ground in a mortar, and C and N were determined in 100-150 mg samples using automated dry combustion (LECO TruSpec CN analyzer).

Soil total phenolic analysis

Ten grams of soil samples (≤ 2 mm) were mixed in 10 ml distilled water and shaken at 22 rotations per minute speed on an over-end reciprocating shaker for 5 h at room temperature. Soil solutions were filtered through Whatman 42 filter paper. Total water-soluble phenols were determined using Folin–Ciocalteu's reagent (Singleton and Rossi 1965). Two hundred and forty microliters of soil solutions were mixed with 15 μL of Folin–Ciocalteu's reagent, allowed to stand for 5 min, then 30 μL of saturated sodium carbonate solution was added, and the mixture was centrifuged at 14,000 *g* for 5 min. A 200 μL volume was pipetted into to a microplate well, and absorbance was read at 725 nm using an xMark^{TM} microplate spectrophotometer.

Soil temperature

Temperature sensors (model DS1922L-F5, precision: 0.5 °C, accuracy: ± 1 °C) were set to record temperatures every 3 h. For installation, the sensors were wrapped in plastic bags to prevent corrosion and buried to 5 cm beneath the soil surface on June 11, 2015. The data were read using a 1-wire viewer on June 9, 2016.

Statistical analysis

Statistical analysis of data was performed using SPSS 19 program (One-way ANOVA), and the Student–Newman–Keuls test was used for post hoc comparisons. Means and standard errors of soil parameters were calculated from each plot. We refer to a P value of ≤ 0.05 as statistically significant and indicate in some cases a P value of ≤ 0.1 as marginally significant. Pearson's correlations were used to estimate the relationship between soil N mineralization, resin N daily availability and soil total phenolics.

Results

Soil chemical properties

Soil pH increased among the soil horizons in the order H < A < B for all vegetation species (Table 1). In the diffuse *P. abies* tree line, the pH of the H and A layers was significantly lower than that of the *P. abies* tree islands, but was not significantly different to *P. abies* at the lower elevation. Between the *P. abies* stands, there was no significant difference in the C or N concentration of the H horizon, but the C/N ratio was significantly higher in the diffuse *P. abies* tree line. In the A horizon, the diffuse *P. abies* tree line had a significantly lower C or N concentration than either the lower elevation closed stand or the tree line tree islands. At the different vegetation types at the tree islands, there was no significant difference in pH, C or N concentration between the *P. abies*, *P. mugo* or *R. ferrugineum.* The C/N ratio was significantly different in the H horizon between *P. mugo* and *R. ferrugineum.* However, the concentration of C, N and C/N ratio decreased consistently in the order H > A > B, and significant differences were shown in the concentration of C and N for all vegetation species in most cases (Table 1).

The summed soil temperature for the growing season was significantly greater in *P. abies* at the lower elevation site than at the tree islands (Fig. S2). At tree line site, *R. ferrugineum* had significant higher soil temperature than *P. abies* or *P. mugo* (Fig. S2). However, the lowest winter soil temperatures (January 2016) were similar both between elevations of the *P. abies* stands and vegetation types at the higher elevation (Fig S1).

N mineralization

Soil net N mineralization under controlled conditions at 20 °C showed that the H horizon of *P. abies* and both elevations and *P. mugo* at the tree line had significantly greater ($P < 0.05$) rates of N mineralization and ammonification compared to the A and B horizons (Fig. 1, Table 3). In the B horizon in all vegetation types and both elevations, very low or negative rates of N mineralization were determined (Fig. 1). In the higher elevation *P. abies*, and *P. mugo* and *R. ferrugineum* in the B horizon soil a lower NH_4^+ value was determined at end of the incubation, compared to the initial value (Table S2). This also occurred in the B horizon soil of the lower elevation *P. abies* (Table S2). At tree islands, a significant difference in net soil N mineralization was found between the different vegetation species. *Picea abies* and *P. mugo* showed a significantly higher N mineralization rate than *R. ferrugineum* in the H horizon; however, no significant differences were found in A and B horizons between different vegetation species (Fig. 1). In *R. ferrugineum*, unlike *P. abies* and *P. mugo* there was no difference in net N mineralization between the H and A horizons (Fig. 1). Rates of ammonification in the H layer were highest in the tree islands *P. abies* and lowest in *R. ferrugineum.* In both the A and B horizon of *R. ferrugineum* and the lower elevation *P. abies*, zero or negative rates of ammonification were shown (Table 2). This was also shown in the B horizon of *P. mugo*. Rates of nitrification were low in all soil horizons, elevation and vegetation types and did not vary between them (Table 2).

Table 1 Chemical properties of soils taken from under *P. abies, P. mugo*, *R. ferrugineum* (June 2015) islands, and a diffuse *P. abies* tree line (June, 2016) (1668–1791 m) and a *P. abies* site (June 2015) at a lower elevation (1395 m) at Wasserberg in the central Alps, Austria

Soil horizons	Lower elevation	Tree line			
	Picea abies	*Picea abies* (diffuse)	*Picea abies* (tree islands)	*Pinus mugo*	*Rhododendron ferrugineum*
Soil pH (water)					
H	4.48 ± 0.08abx	4.3 ± 0.05bx	4.70 ± 0.07ax	4.51 ± 0.05abx	4.67 ± 0.08ax
A	4.65 ± 0.08abxy	4.5 ± 0.03by	4.75 ± 0.05ax	4.61 ± 0.07abxy	4.79 ± 0.11ax
B	4.84 ± 0.08aby		4.77 ± 0.0bx	4.99 ± 0.05ay	4.88 ± 0.12abx
C %					
H	26.8 ± 3.6ax	31.8 ± 3.1ax	24.6 ± 2.2ax	28.7 ± 3.2ax	25.8 ± 2.5ax
A	10.1 ± 1.2by	6.5 ± 0.4cy	12.9 ± 1.6aby	13.7 ± 1.1ay	13.6 ± 1.3aby
B	6.1 ± 0.7az		7.5 ± 1.2az	6.3 ± 0.5az	6.2 ± 0.6az
N %					
H	1.22 ± 0.12ax	1.19 ± 0.1ax	1.24 ± 0.09ax	1.27 ± 0.13ax	1.28 ± 0.10ax
A	0.52 ± 0.06by	0.31 ± 0.02cy	0.66 ± 0.05aby	0.70 ± 0.05ay	0.70 ± 0.05ay
B	0.32 ± 0.03az		0.43 ± 0.05az	0.35 ± 0.03az	0.36 ± 0.03az
C/N					
H	21.4 ± 0.8bx	26.4 ± 0.9ax	20.0 ± 0.8bcx	22.4 ± 0.9bx	19.8 ± 0.7cx
A	19.2 ± 0.6aby	21.4 ± 1.5ay	18.8 ± 0.9bx	19.3 ± 0.6aby	19.0 ± 0.6abx
B	19.2 ± 0.7ay		15.9 ± 1.7by	18.1 ± 0.4aby	17.1 ± 0.7aby

Mean ± SE. Data points within a parameter not followed by the same letter (abc) are significantly different ($P \leq 0.05$) between species or elevation. Data points within a species not followed by the same letter (xy) are significantly different between soil horizons ($P \leq 0.05$), $n = 5$

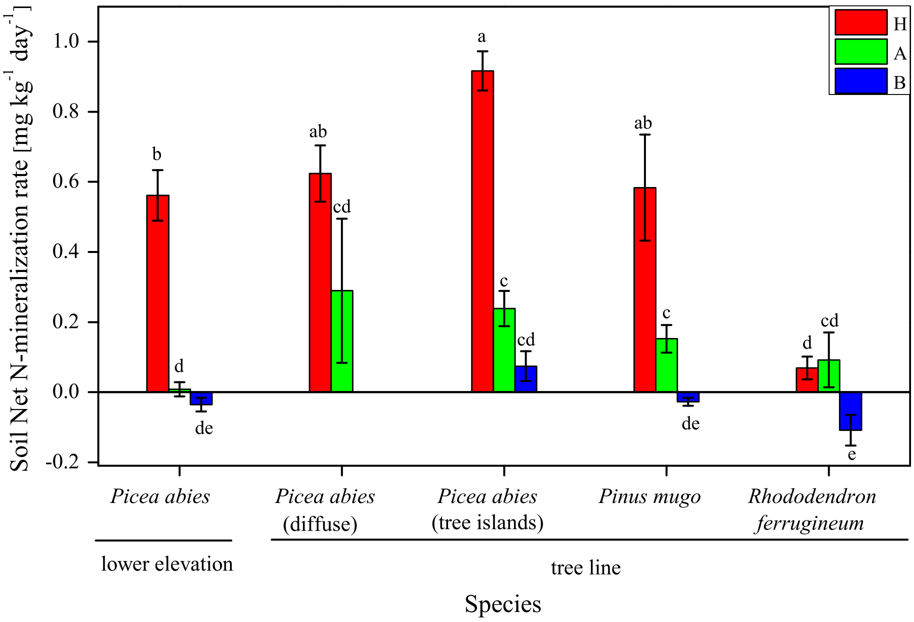


Fig. 1 Net N mineralization (20 °C for 30 days) of different soil layers taken from under islands of *P. abies, P. mugo* and *R. ferrugineum* and diffuse *P. abies* tree line (1668–1791 m) and a *P. abies* site at a lower elevation (1395 m) in June 2015. Bars show mean ± SE. Bars not followed by the same letter are significantly different ($P \leq 0.05$) between species and soil horizons (ab), $n = 5$. Measurement is on a fresh weight basis

Soil in situ N mineralization

Figure 2 shows that there was no significant difference in in situ N mineralization under *P. abies* between the lower elevation and higher elevation, but a significantly greater in situ N mineralization was found under *P. abies* and *P. mugo* compared to *R. ferrugineum* at tree line site. This difference in in situ N mineralization was reflected in the in situ ammonification rate, which was significantly lower under *R. ferrugineum* compared to the other species at the tree line (Fig. 2). There were no significant differences in the rates of nitrification between the different species at the

Table 2 Ammonification and nitrification (20 °C for 30 days) of soils taken from under *P. abies, P. mugo, R. ferrugineum* islands (June 2015) and diffuse *P. abies* tree line (June 2016) (1668–1791 m) and a *P. abies* site (June 2015) at a lower elevation (1395 m) at Wasserberg in the central Alps, Austria

Soil horizons	Lower elevation	Tree line			
	Picea abies	*Picea abies* (diffuse)	*Picea abies* (tree islands)	*Pinus mugo*	*Rhododendron ferrugineum*
Ammonification (mg kg^{-1}day^{-1})					
H	0.55 ± 0.05bx	0.61 ± 0.08bx	0.92 ± 0.04ax	0.47 ± 0.09bx	0.08 ± 0.008cx
A	−0.03 ± 0.01by	0.32 ± 0.2ax	0.23 ± 0.03ay	0.09 ± 0.03aby	−0.009 ± 0.009bx
B	−0.07 ± 0.01by		0.05 ± 0.007az	−0.08 ± 0.03by	−0.05 ± 0.007bx
Nitrification (mg kg^{-1}day^{-1})					
H	0.01 ± 0.03ax	−0.01 ± 0.01ax	−0.002 ± 0.01a	0.11 ± 0.07ax	−0.003 ± 0.03ax
A	0.04 ± 0.01ax	−0.03 ± 0.02ax	0.01 ± 0.02ax	0.06 ± 0.02ax	0.101 ± 0.06ax
B	0.04 ± 0.01abx		0.12 ± 0.04ax	0.04 ± 0.01abx	−0.006 ± 0.04by

Mean ± SE. Data points within a parameter not followed by the same letter (abc) are significantly different between species or elevation. Data points within a species not followed by the same letter (xy) are significantly different between soil horizons ($P \leq 0.05$), $n = 5$. Measurement is on a fresh weight basis

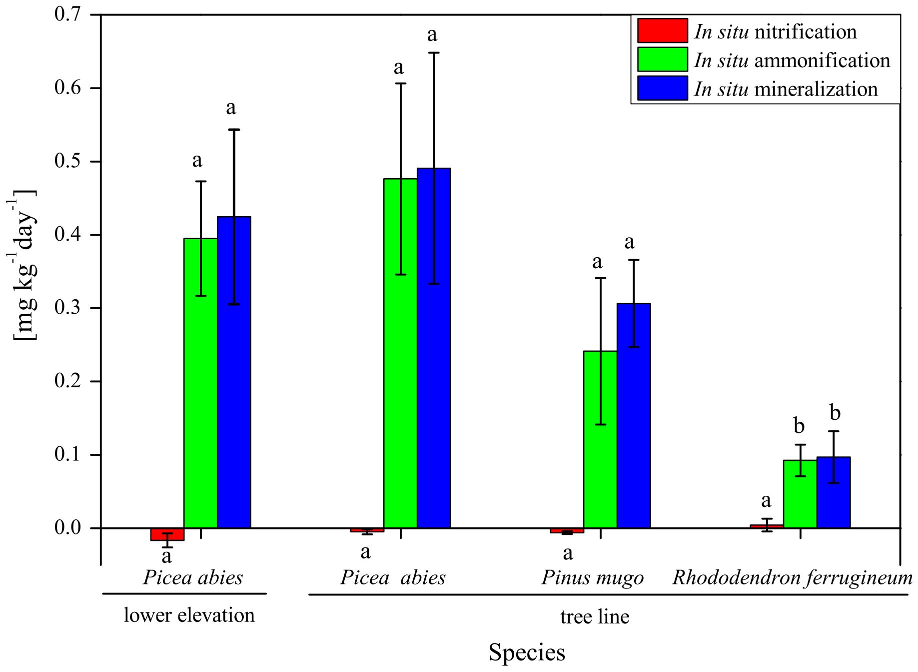


Fig. 2 Net in situ nitrification, net in situ ammonification and net in situ N mineralization of soil to a depth of 12 cm from under islands of *P. abies, P. mugo* and *R. ferrugineum* at the tree line (1668–1791 m) and a *P. abies* site at a lower elevation (1395 m) from June 8 to July 20, 2015. Bars show mean ± SE. Bars not followed by the same letter are significantly different ($P \leq 0.05$) between species (ab), $n = 5$. Measurement is on a fresh weight basis

tree line (Fig. 2). The rates of N mineralization in situ were slightly lower than the rates of net N mineralization determined in the H layer under controlled conditions, but the pattern obtained in the rates of net N mineralization between the different vegetation types and altitude was similar between the incubations done in situ and under controlled conditions (Fig. 1 and 2). Between the controlled condition and the in situ incubations, both the ammonification rates and nitrification rates were comparable (Table 2, Fig. 2).

Soil N availability

Nitrogen availability, determined using ion exchange resin capsules, varied among the different vegetation species (Fig. 3). Figure 3 indicates that there was no difference in NH_4^+ availability but a significant difference in NO_3^- availability between the lower elevation and the tree islands in *P. abies*. At the tree islands, *R. ferrugineum* had a lower amount of resin absorbed total inorganic N compared to *P. abies* (Fig. 3).

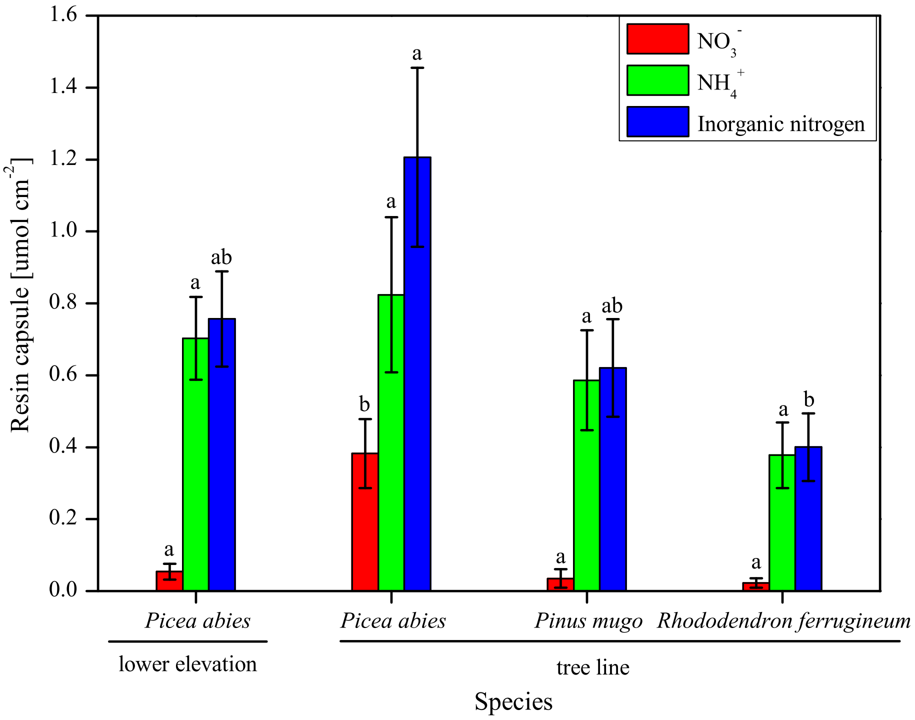


Fig. 3 NH_4^+, NO_3^- measured using resin capsule under islands of *P. abies, P. mugo* and *R. ferrugineum* at the tree line (1668–1791 m) and a *P. abies* site at a lower elevation (1395 m) from June 8 to July 20, 2015. Bars show mean ± SE. Bars not followed by the same letter are significantly different ($P \leq 0.05$) between species (ab), $n = 5$. Measurement is on a fresh weight basis

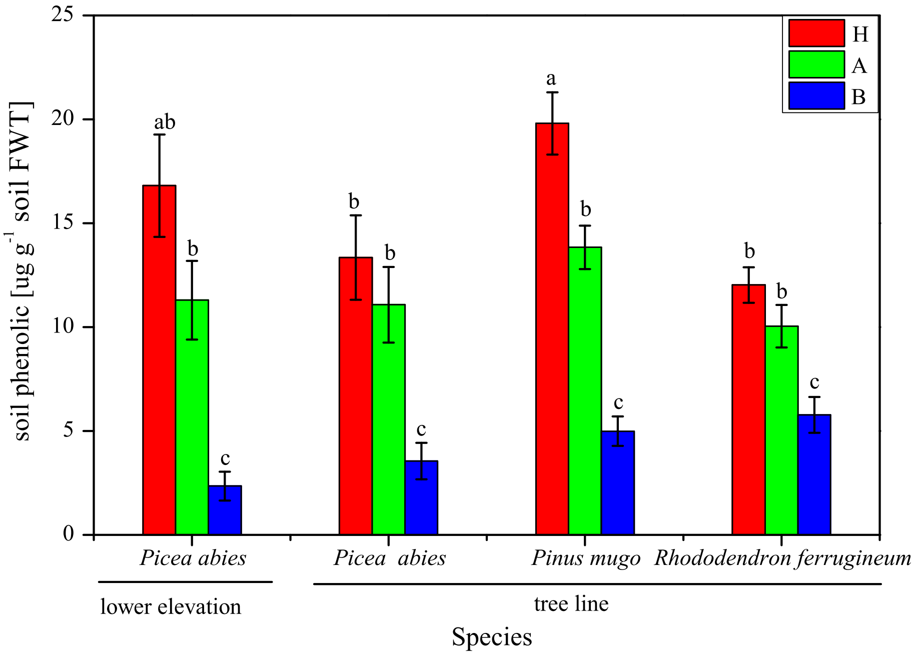
Table 3 Extractable NH_4^+ and NO_3^- of soils taken from under *P. abies, P. mugo, R. ferrugineum* (June 2015) islands and diffuse *P. abies* tree line (June 2016) (1668–1791 m) and a *P. abies* (June 2015) site at a lower elevation (1395 m) at Wasserberg in the central Alps, Austria

Soil horizons	Lower elevation	Tree line			
	Picea abies	*Picea abies* (diffuse)	*Picea abies* (tree islands)	*Pinus mugo*	*Rhododendron ferrugineum*
NH_4^+ (mg kg^{-1})					
H	8.2 ± 0.92bx	0.7 ± 1.8dx	15.9 ± 2.7ax	6.7 ± 1.2bx	2.5 ± 1.1cx
A	1.5 ± 0.3ay	−2.5 ± 2.0ax	4.6 ± 1.0ay	2.2 ± 0.4axy	0.7 ± 0.3bx
B	1.9 ± 0.01ay		2.6 ± 0.04ay	1.1 ± 0.02by	0.7 ± 0.02bx
NO_3^- (mg kg^{-1})					
H	0.9 ± 0.36ax	1.6 ± 0.7ax	0.49 ± 0.22ax	0.22 ± 0.09ax	0.28 ± 0.05ax
A	0.35 ± 0.11ax	1.6 ± 0.7ax	0.98 ± 0.41ax	0.23 ± 0.17ax	0.13 ± 0.03ax
B	0.70 ± 0.19ax		0.37 ± 0.12abx	0.37 ± 0.12bx	0.48 ± 0.2ax

Mean ± SE. Data points within a parameter not followed by the same letter (abc) are significantly different ($P \leq 0.05$) between species or elevation. Data points within a species not followed by the same letter (xy) are significantly different between soil horizons ($P \leq 0.05$), $n = 5$. Measurement is on a fresh weight basis

As shown by the initial extractable values of NH_4^+ and NO_3^- in the N mineralization (Table 3), the levels of extractable NH_4^+ or NO_3^- were significantly different between soil horizons and between some species. At both elevations in *P. abie*s significantly higher extractable NH_4^+ was determined in the H horizon compared to the A and B horizons. In *P. mugo*, a significant difference was shown between the H and B horizon only. In *R. ferrugineum* similar levels of extractable NH_4^+ were determined in all horizons. At both elevations and all vegetation types, no significant differences in the levels of extractable NO_3^- among soil horizons were found. In the H horizon of the diffuse *P. abies* tree line, only very low levels of extractable NH_4^+ were determined. However, this stand had the highest levels of extractable NO_3^- in the H horizon compared to lower elevation or tree island sites. At the tree islands, *R. ferrugineum* had lower amount of extractable NH_4^+ compared to the tree island *P. abies* or *P. mugo* (Table 3).

Fig. 4 Soil total phenolic measured from under islands of *P. abies, P. mugo* and *R. ferrugineum* at the tree line (1668–1791 m) and a *P. abies* site at a lower elevation (1395 m) in June 2015. Bars show mean ± SE. Bars not followed by the same letter are significantly different ($P \leq 0.05$) between species or soil horizons (ab), $n = 5$. Measurement is on a fresh weight basis



Soil total phenolics

In the soil under all species and at both elevations, the amounts of soil water-soluble phenols were significantly higher in the H horizon compared with B horizon (Fig. 4). There were no differences in water-soluble phenols under *P. abies* between the lower elevation and tree islands site in all soil horizons (Fig. 4). At the tree islands site, water-soluble phenols occurred in significantly higher amounts under *P. mugo* in the H and A horizons compared with under *P. abies* and *R. ferrugineum*, but no significant difference was found at B horizon between these vegetation species (Fig. 4). No significant correlation was found between soil N mineralization and soil phenolics ($P = 0.089$, $r^2 = 0.382$).

Discussion

Methodology

Laboratory incubation methods under controlled temperatures (Knoepp and Swank 2002) and field in situ incubation methods (Deluca et al. 2002) are the most frequently used approaches for estimating soil N mineralization (Hanselman et al. 2004). In all soils determined for the different vegetation types and elevations, the rates of N mineralization were similar between the laboratory incubation and the in situ incubation, but the absolute rates differed. On average the rate of N mineralization was ca. 45% higher in the laboratory incubation at 20 °C compared to the in situ incubation. A part of this difference may be due to increased N mineralization through use of homogenized soils in the laboratory incubation compared to the intact cores of the in situ incubation (Hanselman et al. 2004). Also the mean soil temperatures during the in situ incubation were 9.8 °C in the *P. abies* and *P. mugo* soils and 11.0 °C under *R. ferrugineum* at the tree islands site and 11.6 °C in the soil of the lower elevation *P. abies* stand. Several studies have shown that temperature affects rates of N mineralization. Gonçalves and Carlyle (1994) showed that soil N mineralization rate at 13.0 °C was much lower than at 17 °C, and Knoepp and Swank (2002) showed that temperature and temperature–moisture interactions significantly affected net soil N mineralization, and these authors measured maximum N mineralization rates in the summer and autumn when temperatures were highest. Similarly, studies in temperate regions of the world find that N mineralization rates are greatest when soil temperatures are high, in summer and autumn (De Santo et al. 1982; Knoepp and Swank 1995; Nadelhoffer et al. 1984). In addition, even though the tops of the tubes were covered to prevent rain from entering the tubes and flushing them, as the tubes are open at the bottom a loss of N out of the bottom of column by diffusion cannot be ruled out (Hanselman et al. 2004).

Net N mineralization rate in different soil horizons

In all soils, the net N mineralization rates of the humus layer were significantly higher than in the A and B horizons. This result is consistent with those of Persson and Wirén (1995) and MacKown et al. (1987). Persson and

Wirén (1995) showed that the organic horizons contributed 32–74% to total net N mineralization in an acidic forest soil, and MacKown et al. (1987) found that in an agricultural soil 42% of the total estimated N mineralized was derived from the surface soil (0–18 cm), whereas 58% originated from the 18 to 108 cm soil depths. The study of Persson and Wirén (1995) showed that the organic horizon provided most of the inorganic N supplied to plant roots in coniferous forests. In all of the *P. abies* stands both at the lower elevations and at the tree line, as well as in *P. mugo* and *R. ferrugineum* the highest amounts of inorganic N were determined in the H horizon. This suggests that at both the tree line and the lower elevation site the H layer is an important source of inorganic N particularly NH_4^+.

N mineralization rate under different vegetation species

Humus form, N and C content, microbial activity, soil pH and cation exchange capacity are parameters subjected to changes induced by vegetation (Andreetta et al. 2016; Groten and Bruelheide 1997; Miles 1985; Richter et al. 1994; Setälä et al. 2016; Vinton and Burke 1995). These parameters can also affect N mineralization processes (Hanselman et al. 2004; Swift et al. 1979). Marrs et al. (1988) showed in tropical soil that when other limiting factors were lessened under improved conditions (better aeration and moisture and a high incubation temperature) net N mineralization was negatively correlated with soil pH. Correlation analysis (Table S1) also showed that net N mineralization was strongly correlated with soil pH; however, the differences in pH between the soil horizons and vegetation types were small and this relationship may be confounded by other factors. It has been demonstrated that the litter lignin/N ratio explained more of the variation in net N mineralization than climatic factors over a wide range of forest age classes, suggesting that litter quality controls N mineralization by influencing soil organic matter quality throughout the soil profile independent of climate (Scott and Binkley 1997). Thus, differences in litter quality between *R. ferrugineum* and the tree species may have a greater influence than soil pH on net N mineralization.

In both the laboratory incubation under controlled conditions and the in situ field incubation, there were no differences in soil N mineralization rate between tree species at the tree line, but *R. ferrugineum* had a significantly lower rate of N mineralization. DeLuca et al. (2002) showed in boreal forests in Sweden that in areas with high ericaceous cover of *Empetrum hermaphroditum* and *Calluna vulgaris* the rates of N mineralization were lower. In boreal forest, release of phenolic compounds by ericaceous plants has been suggested to limit N availability (Wardle et al. 1997). Rice and Pancholy (1973) showed that condensed tannins, hydrolysable tannins, ellagic acid, gallic acid, digallic acid and commercial tannic acid (hydrolysable tannin) in very small concentrations completely inhibited nitrification by *Nitrosomonas*. Generally, phenolic compounds inhibit microbial processes in either bulk N mineralization or specifically nitrification (Hättenschwiler and Vitousek 2000). In addition in leaves, phenolic compounds may form phenol–protein complexes which in the soil are very resistant to degradation and can inhibit N mineralization (Hättenschwiler and Vitousek 2000). Leaves of ericaceous plants are generally assumed to contain high levels of phenolic compounds (Doche et al. 2005). Adamczyk et al. (2016) showed that roots of *V. vitis-idaea*, *V. myrtillus* and *C. vulgaris* contained higher levels of condensed tannins and total phenols than roots of *Pinus sylvestris*. Doche et al. (2005), however, reported that leaves of *R. ferrugineum* contain much lower levels of tannins compared to leaves of *Vaccinium* (Gallet and Lebreton 1995). At the tree line site, the highest concentration of soil phenolics was found under *P. mugo*, and there were no differences in the content of soil phenolics between *P. abies* and *R. ferrugineum*, but large differences in the rates of N mineralization. Pearson correlation analysis showed no relationship between soil total phenolics and soil N mineralization at the tree line sites. In a study of soil enzymes of the tree line sites (Wang et al. 2017), the activity of enzymes involved in N dynamics such as leucine aminopeptidase and acetyl-glucosaminidase (chitinase) were similar in soils from *P. abies*, *P. mugo* and *R. ferrugineum*, and the activity of phenol oxidase and peroxidase was higher or similar under *R. ferrugineum* than under *P. abies*. In addition, the decomposition rate was also similar for all vegetation types at the tree line (Wang et al. 2017). Thus, there is no evidence of greater inhibition of N mineralization by phenolic compounds under *R. ferrugineum* at the tree line sites.

A characteristic of ericaceous plants is that they have low litter amounts of N and P, which is thought to limit rates of decomposition (Cornelissen et al. 2001), but also other aspects of litter quality such as the content of lignin are known to also play a role (Cornelissen et al. 2001). Maithani et al. (1998) showed that leaves of *Rhododendron arboretum,* which had high lignin levels and low N contents decomposed slowly, while *Schima khasiana* and *Quercus griffithii* leaves, which had high N levels and low lignin contents, decomposed at a faster rate and released N rapidly. These authors concluded that the relatively slow rate of N release from the leaf litter of *Rhododendron arboreum* is due mainly to the sclerophyllous nature of the leaves. The sclerenchyma tissue and the thick cuticle of these leaves are reported to resist enzymatic attack by microbes and physically interfere with the degradation of complex chemicals in the cell walls and thus exert some control over decay and nutrient release rates (Bloomfield et al. 1993). A similar mechanism may explain the significantly lower soil N mineralization determined under *R. ferrugineum*.

Soil N availability

Nitrogen availability is an important factor limiting productivity in most terrestrial ecosystems (Aerts and Chapin III 1999; Vitousek 1982), and the understanding of N dynamics is crucial for natural ecosystems. The levels of extractable inorganic N from NH_4^+ and NO_3^- are a balance between provision of N from N mineralization and N uptake by plant roots and the microbial biomass (Rennenberg and Dannenmann 2015). Both the levels of extractable NH_4^+ in the H layer and the daily available total inorganic N as estimated by the resin capsules were significantly lower under *R. ferrugineum* than under *P. abies* in the tree line islands. This suggests that relative to the rate of N mineralization, the *P. abies* trees of the tree islands have a lower N demand than that of the *R. ferrugineum.* The soil under *R. ferrugineum* had the lowest N availability but also the lowest C/N ratio which should increase the rates of decomposition and N mineralization; thus, these data further support the idea that leaf litter and root litter of *R. ferrugineum* contain a high amount of recalcitrant compounds (Wurzburger and Hendrick 2007) that retard decomposition and N mineralization throughout the soil profile (Scott and Binkley 1997). This is in accordance with the lower daily N availability shown in the soil from under *R. ferrugineum* and also corresponds to lower N mineralization obtained in the soil. The very low level of extractable NH_4^+ in the H layer of the diffuse *P. abies* tree line is an indication that N demand is higher relative to the supply by N mineralization in these stands. The negative rates of ammonification measured in the A and B soil layers of *P. abies* at the lower elevation and *R. ferrugineum* are evidence of microbial immobilization in these soils. Again for *R. ferrugineum* this suggests a tight N cycle under these plants (Wurzburger and Hendrick 2007) and also N limitation in the *P. abies* at the lower elevation. If the tree systems are compared, then both the diffuse *P. abies* tree line and the lower elevation stand would appear to be more N limited than either the tree island *P. abies* or the *P. mugo*. This is an indication that N limitation at the tree line may be both context dependent and dependent upon the form of tree line investigated.

Conclusions

The results of this study show N mineralization rates are similar in *P. abies* and *P. mugo* at the tree line regardless of tree line form. Rates of N mineralization are lower under *R. ferrugineum* than the tree species, but this lower rate is not related to the occurrence of high level of total phenols in the soil. Nitrogen deficiency was not evident in the island-type tree line, but was evident in the diffuse tree line type.

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