Heterotrophic respiration and nitrogen mineralisation in soils of Norway spruce, Scots pine and silver birch stands in contrasting climates

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Abstract

Different tree species are often associated with different soil properties. Earlier studies have shown that Norway spruce (*Picea abies* (L.) Karst.) and Scots pine *(Pinus sylvestris* L.), the two dominant tree species in Fennoscandia, often generate soils with larger carbon (C) and nitrogen (N) pools than silver birch (*Betula pendula* Roth.). Consequently, we hypothesised that spruce and pine would create soils with slower turnover rates than birch. To test this, C and N pools and C and N mineralisation rates were determined in different soil layers (humus, 0–10 cm, 10–20 cm mineral soil) at two sites with contrasting climatic conditions. One site (Tönnersjöheden) was located in the temperate zone in SW Sweden and one (Kivalo) in the north boreal zone in N Finland. At both sites, experimental plots with the three tree species had been established more than 50 years before the study. Samples from the different soil layers were incubated at 15 °C in the laboratory for 30 days, and C and N mineralisation rates were determined. In addition, earthworm abundance was estimated at Tönnersjöheden but not at Kivalo (no sign of bioturbation). At Tönnersjöheden, soil C and N pools (g C or N m^{-2}) were ranked spruce>pine>birch. C mineralisation rate (mg CO_2-C g^{-1} C d^{-1}) was higher in the birch plots than in the other plots, but because of larger C pools in the spruce plots, field C mineralisation (g CO_2-C m^{-2} yr^{-1}) was higher for spruce than for pine and birch. Field net N mineralisation (80-90 kg N ha^{-1} yr^{-1}) did not differ significantly between tree species, but nitrification rates (µg NO_3-N g^{-1} C d^{-1}) in the topsoil were higher in the birch plots than in the other plots. The birch plots had larger populations of earthworms and a higher degree of bioturbation than any of the coniferous plots, which probably explains the higher turnover rate of birch soil organic matter (SOM). At Kivalo, C and N soil pools were significantly larger in spruce than in birch plots, and C mineralisation rate was higher in birch and spruce humus than in pine humus. Net N mineralisation rate and annual field net N mineralisation (<4 kg N ha^{-1} yr^{-1}) were estimated to be very low, with no effect of tree species. Thus, the hypothesis of a 'birch effect' was supported at Tönnersjöheden, but only partly at Kivalo. The main difference seemed to be that the earthworms at Tönnersjöheden accelerated SOM decomposition under birch, whereas earthworm stimulation was negligible at Kivalo, probably because of climate-related limitations.

Keywords

Carbon mineralisation, nitrogen mineralisation, *Picea abies, Pinus sylvestris, Betula pendula,* earthworms

1. Introduction

Different tree species growing on similar sites often differ in productivity, canopy structure and the quality and quantity of litter. This is the case for the main forest trees growing on acid forest soils in northern Europe – Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth.).

Even though these species are able to grow on a wide range of site types, forest management has tended to restrict the species to sites where their timber production potential is greatest (Helmisaari et al., 2009). For example, Norway spruce normally has higher production than Scots pine and silver birch on fertile, mesic sites, while Scots pine is grown on relatively infertile, more coarser-textured soils (Ekö et al., 2008). Silver birch and Scots pine have lower leaf area index than Norway spruce, allowing more solar radiation to reach the ground, and therefore often have more developed understorey and ground vegetation than spruce forests. The tree species also affect ground vegetation and soil carbon (C) and nitrogen (N) turnover through litter and throughfall chemistry (Barbier et al., 2008) and microclimate, e.g. soil moisture and temperature. These factors in turn influence the composition of soil organisms and their effect on soil bioturbation. Deciduous trees are thus often associated with a greater abundance of soil-mixing earthworms, which are normally less abundant in soils under coniferous stands.

The current trends towards a warmer climate will probably alter the natural distribution of tree species in northern Europe, but may also have implications for the choice of tree species in forest management. Furthermore, there are reasons to expect several interactions and feedback connections between tree species, climate change and soil C sequestration. Many processes determine C sequestration rate, as it is the result of a balance between litter input on one hand and decomposition of soil organic carbon (SOC) and leaching of dissolved organic carbon (DOC) on the other.

68 The balance between litter production and decomposition rate largely determines the rate of change in
69 SOC pools. Hansson et al. (2011) found that SOC storage was significantly greater in Norway spruce
70 plots than in adjacent Scots pine and silver birch plots in the temperate zone of SW Sweden. In
71 addition, total N storage was greater under spruce than under birch. The greater basal area and above-
72 ground litterfall in the spruce plots indicated higher production rates. Decomposition rates were not
73 measured, but higher decomposition rate of birch leaves than of pine and spruce needle litter is a
74 possible explanation for the much lower SOC pool in the birch humus layer. Furthermore, the
75 understorey vegetation in pine and birch plots was dominated by graminoids, forbs and ericacean
76 dwarf shrubs, whereas only mosses occurred in the spruce plots. In the north boreal zone of Finland,
77 Smolander and Kitunen (2002) and Kanerva and Smolander (2007) observed lower microbial activity
78 in terms of heterotrophic respiration in the humus layer of Scots pine compared with adjacent Norway
79 spruce and silver birch plots.
80
81 The aim of the present study was to determine C mineralisation (heterotrophic respiration) and net N
82 mineralisation in soils at the sites studied by Hansson et al. (2011) in Sweden and Kanerva and
83 Smolander (2007) in Finland in order to detect possible differences in these variables between tree
84 species and between geographical positions. C and net N mineralisation in soils from the two sites was
85 measured using laboratory incubations at constant temperature (15 °C) over 30 days, and the annual
86 field mineralisation rates were calculated according to methods described by Kutsch et al. (2010). The
87 abundance of earthworms was only estimated at the Swedish site, since the structure of the humus
88 layer suggested that earthworms were abundant in some plots at that site but not at the Finnish site.
89 However, earthworms were excluded from the incubation study for reasons of comparison. The
90 incubation study thus primarily examined the influence of tree species on the quality of the soil
91 organic matter (SOM) and the microbial community. Our principal hypotheses were:
92 (1) C and net N mineralisation rate per unit C is determined by substrate quality, which was expected
93 to decrease in the order birch > spruce > pine.
94 (2) Field mineralisation per unit area is also determined by the accumulated pools of C and N in soil.

Specifically, we expected that stands of Norway spruce and Scots pine would create soils with larger pools of C and N and slower turnover rate than stands of silver birch.

2. Materials and methods

2.1. Study sites

Two study sites were used, one located in SW Sweden at Tönnersjöheden (56°40'N, 13°03'E) and the other in N Finland at Kivalo (66°20'N, 26°40'E), close to the Arctic circle.

The climate at Tönnersjöheden is temperate with mild winters due to the marine influence. Mean annual air temperature is 6.4 °C, and mean annual precipitation is 1053 mm (Alexandersson et al., 1991). The duration of the growing season (>5 °C) is 204 days (Olsson and Staaf, 1995). The soils at Tönnersjöheden have a glacifluvial origin and overlie the Precambrian bedrock (Malmström, 1937; Hansson *et al*., 2011). Most experimental plots used in the study showed signs of podzolisation, although only one fulfilled all the criteria to be classified as a Podzol according to IUSS Working Group WRB (2006). Five plots were classified as regosols and two as arenosols. A detailed description of the soils and stand history of Tönnersjöheden can be found in Hansson et al. (2011).

Kivalo is situated in the sub-Arctic climatic region with a short growing season (136 days) and long, cold winters with a snow cover in the order of 1 m. Mean annual precipitation is 561 mm and mean annual air temperature is 1.7 °C (Ostonen et al., 2007; Helmisaari et al., 2009). The soils at Kivalo are glacial till soils on Precambrian bedrock. The soil type is podzolic with mor humus and vegetation of the *Hylocomium-Myrtillus* type (Cajander, 1949).

2.2. Experimental design and stand characteristics

The experimental design at Tönnersjöheden included plots of the tree species Norway spruce, Scots pine and silver birch replicated in a block design (n=3 except for birch, where n=2). The plot size was in the range 720-1080 m^2. Most plots used in the study were established as parts of older experiments, but the previous treatments, which concerned provenance and thinning (last planned thinning in 2002 and an additional thinning after storm damage in one plot in 2005), were considered to cause no bias for the present study. The stands of the present plots in the study area were established in 1951-1963, and thus stand age at sampling ranged between 46 and 58 years. The basal area of the established overstorey trees varied from 12.3 to 37.5 m^2 ha^{-1} in 2009/2010, and was on average 15.4, 21.6 and 29.3 m^2 ha^{-1} in birch, pine and spruce plots, respectively. The understorey vegetation in the Scots pine and silver birch plots consisted of suppressed trees (e.g. *P. abies*, *Fagus sylvatica*, *Quercus robur, Sorbus aucuparia, B. pendula*), bushes (e.g. *Frangula alnus*) and well-developed field layers of e.g. *Vaccinium myrtillus*, *V. vitis-idaea, Deschampsia flexuosa*, *Calluna vulgaris* and *Agrostis capillaris*. In the Norway spruce plots, the ground vegetation was restricted to a bottom layer of mosses, e.g. *Dicranum* spp. and *Hypnum cupressiforme.*

The experimental design of the Kivalo site consisted of the same tree species as at Tönnersjöheden, with three replicate plots (n=3) in each stand. The plot size was 625 m^2. In contrast to Tönnersjöheden, the stands at Kivalo were not replicated, but each stand contained replicate plots. The birch stand was naturally regenerated, the spruce stand was planted in 1930 and the pine stand was established after unsuccessful spruce regeneration, where pine was favoured at clearing. Thus, stand age at sampling was 79 years. All stands were established after clear-felling a Norway spruce stand followed by prescribed burning in 1926. At the time of the study by Smolander and Kitunen (2002), the basal area of the tree layer was 21.3, 22.0 and 28.4 m^2 ha^{-1} in the birch, pine and spruce stands, respectively. The pine stands included 1.3 m^2 ha^{-1} of birch and the spruce stands included 5.4 m^2 ha^{-1} of birch and 3 m^2 ha^{-1} of pine. The understorey vegetation was dominated by *V. myrtillus*, but low herbs and grasses

were more abundant in the birch stand than in the coniferous stands, and the bottom layer of mosses was more homogeneous in the spruce stand (Smolander and Kitunen, 2002).

2.3. Soil sampling

Soil sampling at Tönnersjöheden was carried out in late August 2009. In each plot, the humus layer was sampled using a 70-mm steel corer at 15 random spots. Spots allotted to superficial stones, stumps or stem bases (< 50 cm distance from trees) were replaced by other spots to obtain 15 samples. The mineral soil was sampled at the same spots using a 25-mm steel corer, and the soil cores were divided in the field into 0-10, 10-20 and 20-30 cm soil layers. The 15 samples from each soil layer were pooled except for the deepest layer, where only 5-10 samples were taken due to high stoniness. Because the fresh litter layer (Oi) was thin and interwoven with mosses and other plants, this layer was excluded from the study. Fragmented litter (Oe) was included in the humus layer. The humus layer had an average depth of 2.1, 4.7 and 6.7 cm in the birch, pine and spruce plots, respectively.

Soil sampling at Kivalo was carried out in September 2009. Ten soil cores were randomly taken from the humus layer (Oe + Oa) of each of the nine plots, using a cylindrical soil corer (60-mm diam.), while 5-7 cores were taken from the mineral soil layer. The mineral soil cores were divided into 0-10 and 10-20 cm soil layers. The humus layer had an average depth of 2.9, 2.3 and 2.7 cm in the birch, pine and spruce plots, respectively.

Some of the soil cores at the spots selected for sampling could not be taken to the full mineral soil depth of 30 cm at Tönnersjöheden or 20 cm at Kivalo because of stones. The amount of fine soil (i.e. < 2 mm, see below) was therefore only calculated for those cores that were successfully pushed through a specific soil layer. This amount of soil was then reduced according to the degree of stoniness as determined according to the method of Stendahl et al. (2009) modified from Viro (1952).

An additional sampling of the soils at Tönnersjöheden was made in September 2010 to determine the abundance of earthworms (Oligochaeta). In each plot, samples of the litter and soil were taken from 5 spots, located in the same manner as in the previous soil sampling, using a circular steel template (250 cm^2). Starting from the litter surface, samples were taken from the 0-5, 5-10 and 10-15 cm soil layers by carefully excavating the soil material. At the sampling occasion, all soil layers were moist, which is often a prerequisite for earthworm presence in the topsoil.

2.4. Laboratory treatment

All samples were transported in cooling boxes to the laboratory, where they were stored fresh at 4-5 °C during the preparation process before the final analyses. Live roots were removed by hand and the samples were passed through a 5-mm (humus samples) or a 2-mm (mineral soil) mesh. This procedure (1) increased soil sample homogeneity and (2) removed living fragments of roots and mycorrhiza to avoid "autotrophic" respiration.

The fresh material from each sample was carefully mixed and was divided into a number of sub-samples to be used to determine: (i) dry matter content, (ii) soil pH, (iii) total C and N concentrations, and (iv) inorganic N concentration. In addition, another sub-sample was removed for C and N mineralisation studies. Water-holding capacity was assumed to be the same as for the nearby Skogaby site (Persson et al., 2000). The analytical procedures for (i-iv) above were:

i) Fresh weight/dry weight ratio was determined after the sub-samples were dried at 105 °C for 24 h.

ii) Soil layer pH was determined with a glass electrode in the supernatant after shaking for 2 h on a rotary shaker and sedimentation in an open flask for another 22 h. The relative proportions of fresh soil and distilled water were 1:1 by volume (about 1:10 by weight of dry matter to water for humus and 1:2.5 for mineral soil).

iii) Soil samples were vacuum-dried at 60 °C for 24 h prior to analysis of total C and N concentration, which was made by dry oxidation using a Carlo-Erba NA 1500 Analyser.

iv) Inorganic N was extracted by agitating mixtures of 10 g humus material or 20 g mineral soil and 100 ml of 1 M KCl solution for 1 h on a rotary shaker. After filtration through Munktell filter papers (0K), the filtrate was photometrically analysed for NH_4^+-N and NO_2^--N + NO_3^--N on a FIA STAR 5010 Analyser.

2.5. Mineralisation study

After sample preparation, which was completed in about 3 weeks, each humus and mineral soil subsample (corresponding to 16 and 100 g dry wt, respectively) was placed in a plastic container (50 cm^2 surface area, 466 cm^3 volume) fitted with a lid with a 5-mm diameter aperture for gas exchange. These soil microcosms were incubated at a constant temperature of 15 °C. The soil moisture level was set to 60% of the water holding capacity (WHC), either by addition of distilled water to dry samples or by letting wet samples dry up to the appropriate water content. A full incubation period lasted for 30 days. CO_2 measurements were performed once a week after the starting day, and the mean CO_2 evolution rate per day was based on cumulative estimates up to day 30.

To determine C mineralisation in the soil sample, the container lid was periodically replaced with an airtight lid with a rubber septum. Background gas samples were taken after 15 minutes from the headspace with a syringe and were injected into a gas chromatograph (Hewlett Packard 5890, H.P. Company, Avondale, PA, USA). The measurements were repeated when an appropriate amount of CO_2 had accumulated in the containers, from 2 h (humus) to about 5 h (mineral soil), depending on the respiration rate. The mass of C evolved per container and hour was calculated according to Persson et al. (1989) and Persson and Wirén (1993), taking the pH-dependent solubility of CO_2 in the soil water into account.

C mineralisation rate was generally expressed as g CO_2-C g^{-1} C d^{-1}, and quantitative data on the C pools in each soil layer enabled C mineralisation rates per m^2 to be calculated. Because roots and mycorrhizal mycelia were partly removed by sieving, and since there was a delay of 3 weeks between sampling and start of incubation, we considered the estimated C mineralisation to be of heterotrophic and not autotrophic origin.

Potential net N mineralisation and nitrification were calculated using the following equations (Robertson *et al*., 1999): Potential net N mineralisation = $[(NH_4^+–N + NO_3^–N)_f - (NH_4^+–N + NO_3^–N)_i]/T_d$; and potential net nitrification = $[(NO_3^–N)_f - (NO_3^–N)_i]/T_d$, where the subscripts i and f indicate concentrations measured before and after aerobic incubation, respectively, and T_d indicates incubation time in days. A negative value indicates microbial net immobilisation. Potential net N mineralisation and nitrification rates were expressed as μg N g^{-1} C d^{-1}.

2.6. Extrapolation to the field

Extrapolation to the field was made by multiplying estimates of C mineralisation, net N mineralisation and net nitrification rates obtained in the laboratory at 15 °C (expressed per g of C) by: (1) the amount of C per soil layer, (2) the number of days per year (365), (3) a temperature-dependent factor (F_{ST}) and (4) a moisture-dependent factor (F_{SM}). F_{ST} (Eq. 1) was calculated for each soil layer and month (Persson et al., 2000) with input data on soil temperature (ST) measured at 10 cm depth (Skogaby, close to Tönnersjöheden, and Kivalo). F_{SM} (Eq. 2) was calculated for each soil layer and month with input data on soil moisture (SM) measured at 10 cm depth at Skogaby and 20 cm depth at Kivalo. The response function for soil moisture (F_{SM}) was based on Seyferth (1998), who found a linear relationship between relative water content (x) and C mineralisation rate.

$$F_{ST} = (ST - T_{min})^2 / (T_{ref} - T_{min})^2 \quad (1)$$

$$F_{SM} = 0.8x + 0.2 \quad (2)$$

where ST is the soil temperature in the field (°C), T_{min} is -6.2 (°C), T_{ref} is the laboratory incubation temperature (15 °C), and x = fraction of optimum soil moisture (our laboratory condition of 60%

WHC was considered as 1, as was the winter moisture at Skogaby and Kivalo of 70% water content in the humus layer and about 30% in the upper mineral soil). After integration for the whole year, the correction factor for converting the rates obtained in the laboratory at 15 °C and 60 % WHC to those in the field soil (F_{ST} * F_{SM}) was estimated to be 0.35 for Tönnersjöheden and 0.26 (pine) and 0.24 (spruce and birch) at Kivalo. The same correction factor was used for both C and net N mineralisation.

2.7. Soil fauna

The soil samples for earthworm extraction were individually spread out on 20-cm × 20-cm nets with 5-mm mesh in Tullgren funnels, extracted for 3 days and collected in 80% ethanol. Tullgren funnels, which are not generally recommended for earthworms, seem to be highly efficient for the extraction of *Dendrobaena* species from mor humus, provided that the inside of the funnel walls is inspected for adhering worms (Malmström et al., 2009). The animals were counted and determined to species under a binocular microscope.

2.8. Statistical analysis

The data from Tönnersjöheden was statistically analysed using an ANOVA procedure where blocks and tree species were taken as sources of variation. Proc MIXED in SAS software was used in the statistical analyses. At Kivalo, tree species were not replicated in a block design but each stand contained replicate plots. The effect of tree species at Kivalo was, therefore, tested with paired samples t-test. Results are reported as significant when $p<0.05$.

3. Results

3.1. C and N soil pools and soil pH

Total amounts of C and N (g m^{-2}) in the humus layer at Tönnersjöheden were significantly larger ($p<0.05$) in the spruce plots than in the pine plots and were larger in both of these than in the birch plots (Fig. 1). Similar differences between tree species were observed for total C pools to a depth of 20 cm in the mineral soil. Total N pools in the soil profile were significantly larger in the spruce plots than in the pine and birch plots. C and N pools in all soil layers at Kivalo were generally smaller than at Tönnersjöheden, and the total amounts of both C and N were significantly larger in spruce plots than in birch plots. The C:N ratio was generally higher at Kivalo than at Tönnersjöheden, and differences between tree species were largest in the humus layer (Table 1). The C:N ratio of the humus layers was lower in birch plots than pine plots at both sites, and at Tönnersjöheden the birch plots had also lower values than the pine plots ($p<0.05$). Soil pH was generally higher at Kivalo than at Tönnersjöheden and pH was generally lower in spruce than in birch humus (Table 1).

3.2. C and N mineralisation rate

C mineralisation rate (mg CO_2-C g^{-1} C d^{-1}), determined at 15 °C in the laboratory, was generally highest in the humus layer and decreased with increasing soil depth at both sites (Fig. 2). The pine plots at Kivalo were an exception, where C mineralisation rates were almost identical in the humus and the 0-10 cm mineral soil layer. C mineralisation rate in the humus layer at Tönnersjöheden was about three-fold higher in the birch plots than in the pine and spruce plots. In contrast, the C mineralisation rate in the humus layer of the birch plots at Kivalo did not differ significantly from that in the spruce plots, whereas the pine plots had lower ($p<0.05$) C mineralisation rate.

At both sites, there were no significant differences between tree species in the mineral soil. With the exception of the high C mineralisation rate in the birch humus layer at Tönnersjöheden and the low C mineralisation rate in the pine plots at Kivalo, the C mineralisation rates were higher in comparable humus and mineral soil layers from Kivalo than from Tönnersjöheden.

Net N mineralisation rate (mg N g^{-1} C d^{-1}) at Tönnersjöheden, determined at 15 °C in the laboratory, followed the same pattern as for C mineralisation rate, with higher rates in the humus layer than in the deeper soil layers (Fig. 3). N mineralisation rate at this site was significantly higher ($p<0.05$) in the birch plots than in the pine and spruce plots in both the organic and the 0-10 cm mineral soil layer, and tended to be so even in the 10-20 cm layer. Most inorganic N produced in the humus layer was in the form of ammonium, and net ammonium production was higher ($p<0.05$) in birch humus than in coniferous humus (Table 2). Nitrification occurred mostly in soils of the pine and birch plots. More nitrate was formed in pine than spruce humus, but in the uppermost mineral soil (0-10 cm) nitrification rate was higher (mg NO_3-N g^{-1} C d^{-1}) under birch than under conifers. In contrast, the overall net N mineralisation at Kivalo was very low, and there were also negative values, particularly in the humus layer in the spruce plots, indicating net immobilisation during the incubation situation (Fig. 3). Nitrification was negligible (Table 2). The greatest variation was observed in the humus layer in the birch plots.

3.3. Field C and N mineralisation

At both Tönnersjöheden and Kivalo, annual field C mineralisation (heterotrophic respiration, g CO_2-C m^{-2} yr^{-1}) in the humus and 0-20 cm mineral soil layers combined was estimated to be significantly higher in the spruce plots than in the pine plots, and C mineralisation was also higher in spruce plots than in birch plots at Tönnersjöheden (Fig. 4). This difference could be due to the significantly larger C pool in the humus layer at Tönnersjöheden despite the relatively low C mineralisation rate in the same layer. At Kivalo, the higher mineralisation in the spruce plots was primarily due to slightly higher C mineralisation rate in combination with a tendency for a larger C pool. There was also a significant difference in annual field C mineralisation between pine and birch stands in the 0-10 cm mineral soil.

Field net N mineralisation at Tönnersjöheden combined for the humus and 0-20 cm mineral soil layers was substantial, 8-9 g N m^{-2} yr^{-1}, but there was no difference between tree species (Fig. 5). However,

there were significant differences between tree species and soil layers in the relative proportions of ammonium and nitrate. There were differences between soil layers, as net N mineralisation was dominated by the humus layer in the spruce and pine plots, whereas the humus and the 0-10 cm mineral soil layer were of equal importance in the birch plots. The field net N mineralisation at Kivalo was very low, and there were no differences between tree species for any soil layer.

3.4. Earthworm abundance and biomass

The overall abundance of earthworms was significantly higher in the birch plots than in the coniferous plots. *Dendrobaena octaedra* (Savigny) was the most abundant earthworm species at Tönnersjöheden (Fig. 6). The abundance of *Lumbricus rubellus* (Hoffmeister), which was only found in the pine and birch plots, was also higher in the birch plots. Juveniles and adults of the two species were approximately equally abundant (not shown). Because *L. rubellus* is about 5-10 times larger than *D. octaedra*, the earthworm biomass was much higher in the birch plots than in the coniferous plots.

4. Discussion

The results clearly indicated that the effects of tree species on soil properties were more pronounced at the temperate Tönnersjöheden site than at the boreal Kivalo site, and the effects were mostly confined to the humus layer. The hypothesis that birch stands would create soils with more rapid turnover and lower SOM pools than the conifer stands was supported at Tönnersjöheden. However, the results from Kivalo gave little support for the hypothesis, as differences in heterotrophic activity were most marked between pine on one hand and spruce and birch on the other, rather than between conifers and birch, which was the case at Tönnersjöheden.

Differences in canopy structure of the tree species may have caused different soil temperatures. Based on measured soil temperatures of different stands at Kivalo, this effect was compensated for in the correction factor for scaling up from laboratory (15 °C) to annual respiration in the field. However, soil temperature data from the different stands at Tönnersjöheden were lacking, and instead temperature data from the adjacent spruce stands at Skogaby was used for all stands. This means that mineralisation rates of the birch and pine stands at Tönnersjöheden may have been underestimated. On the other hand, differences in soil temperatures were probably small, since the field-layer vegetation was much more developed in these stands than in the spruce stands.

The difference between sites means that there were different underlying causes for the seemingly general result that field C mineralisation was greater in spruce than in pine plots at both Kivalo and Tönnersjöheden. At the latter site, the higher field C mineralisation in spruce stands was an effect of larger C pools in the humus layer, whereas at Kivalo the effect was due to higher heterotrophic activity in spruce humus than in pine humus.

The differences between tree species observed at Kivalo in the present study agree with results from a previous study at the same site by Smolander and Kitunen (2002). They found C mineralisation rate per unit organic matter (OM) and day, measured in a 2-week incubation at 14 °C, to be higher in the spruce and birch organic layer than in that of pine stands, and their estimated values were close to those found in the present study. On the other hand, they reported significantly higher net N mineralisation in the organic layer of the birch plot than in the pine plot, and their estimates were much higher than in the present study. This difference can probably be explained by the longer incubation period in their N mineralisation study (13 weeks) than in ours (30 days), because a long incubation without any supply of external C or N will probably reduce microbial production and favour net N mineralisation over net immobilisation.

Kanerva and Smolander (2007) studied C and N mineralisation at Kivalo in incubation experiments over 8 (C) and 10 weeks (N). C mineralisation rate was higher in spruce and birch plots than in pine

391 plots for all organic soil layers, and the values decreased by almost one order of magnitude from the
392 litter layer (Oi) to the bottom of the humus layer (Oa). C mineralisation rate of the intermediate F layer
393 (Oe) was close to values in the humus (FH) layer reported by Smolander and Kitunen (2002) and in
394 the present study. Net N mineralisation was highest in the F layer, where the rates were substantially
395 higher in spruce and birch than in pine materials. The overall conclusion was that spruce and birch
396 humus was more active than pine humus. Differences between tree species may also be partly related
397 to differences in vegetation and in the litter produced; the moss cover was most homogeneous in the
398 pine plots (Smolander and Kitunen, 2002; Kanerva and Smolander, 2007). Studies of tundra soils
399 show that thicker moss cover affects microbial biomass and activity, resulting in colder soil and less
400 plant-available N (Gornall et al., 2007). Such effects are probably also applicable to north boreal
401 forests.
402
403 At Tönnersjöheden, the birch plots differed in particular from the spruce plots, whereas the pine plots
404 sometimes had an intermediate position. Three main differences between tree species could be found
405 at Tönnersjöheden: (1) C and N mineralisation rates per unit C and day were higher in birch than in
406 conifer organic layers; (2) nitrate was the major inorganic N form in birch soil in contrast to conifer
407 soils, although field N mineralisation was almost the same in soils of all tree species; and (3)
408 earthworm populations were clearly larger in birch soils than in conifer soils. The first (1) observation
409 agree with the study of Vesterdal et al. (2012) in Denmark. They found lower heterotrophic respiration
410 (mg C g^{-1} C d^{-1}) in the topsoil of Norway spruce than in soils under 5 broadleaved species (not birch,
411 though) as well as lower ratios between foliar litterfall C and forest floor C.
412
413 The greater abundance of earthworms in the birch plots at Tönnersjöheden is probably the single most
414 important cause of the tree-species differences in C and N mineralisation, as the presence of
415 earthworms is known to increase decomposition (Haimi and Huhta, 1990). The two earthworm species
416 found, *D. octaedra* and *L. rubellus*, are abundant in mesic forest soils in North Europe and are also
417 important invasive species in temperate and boreal forests of North America, along with other
418 earthworms native to Europe (Addison, 2009). Due to their tolerance to moderate acidity, frost and

419 relatively poor food, they are common earthworms in moderately acid coniferous soils in Finland and
420 Sweden. The larger *L. rubellus* is less frost-tolerant than *D. octaedra,* which is why it probably does
421 not occur in N Finland, e.g. in Kivalo (Terhivuo and Valovirta, 1978). However, we did not
422 investigate earthworm occurrence at Kivalo, since the raw humus character of the soils of all tree
423 species indicated no or negligible earthworm activity.
424
425 Many field and laboratory studies have demonstrated the capacity of *D. octaedra*, *L. rubellus* and
426 other detritus-feeding earthworms of the forest floor to dramatically change soil conditions if
427 population densities increase (e.g. Frelich et al., 2006; Haimi and Huhta, 1990; Hale et al., 2005;
428 McLean and Parkinson, 2000; Saetre, 1998; Scheu and Parkinson, 1994). Both species consume
429 detritus and are litter-dwelling (epigeic), but in addition, the epi-endogeic *L. rubellis* has some
430 capacity to mix mineral soil with the organic horizon. Thus, the more blurred transition between the
431 organic layer and the mineral soil in the birch plots at Tönnersjöheden agrees with the occurrence of *L.*
432 *rubellus* (Hansson et al., 2011). Although they are comparatively acid-tolerant and can feed on
433 coniferous litter, they reach higher population densities when feeding on deciduous and herbaceous
434 litter. Liming to increase soil pH can cause significant and long-term increases in population densities
435 (Kreutzer, 1995; Persson et al., 1996). In an initial invasion in aspen forests in Canada, population
436 densities of *D. octaedra* were very high, 2,621 individuals per m^2, but then dropped to 76 individuals
437 per m^2 within a few years (Dymond et al., 1997). The lower figure is typical of northern European
438 forests and also similar to the populations in the birch plots at Tönnersjöheden. Both *D. octaedra* and
439 *L. rubellus* clearly feed well on birch litter. In a microcosm experiment where raw humus was added
440 with senescent birch leaves, *L. rubellus* consumed whole birch leaves except for the petiole, whereas
441 *D. octaedra* ripped the soft parts of leaves (Haimi and Huhta, 1990). As a result, the worms increased
442 microbial respiration (*D. octaedra* only slightly) and N mineralisation and raised the pH of leachate
443 water and humus; *L. rubellus* by 0.2-0.6 pH units and *D. octaedra* by 0.1-0.4 units. The abundance of
444 earthworms in birch plots at Tönnersjöheden was of a similar order of magnitude to that reported for
445 30-year-old birch following spruce in central Finland (62°N) (Räty and Huhta, 2004).
446

447 No earthworms were present in soil samples in our incubation experiment, but differences in C
448 respiration and N mineralisation reflected differences in microbial activity and soil organic matter
449 quality, which was influenced by the earthworms. Furthermore, the higher rate of nitrification in the
450 birch soil can be expected from the lower C/N ratio and the higher pH of the soil in birch plots.
451
452 Tönnersjöheden and Kivalo differed markedly in net N mineralisation rate. The high estimated field N
453 mineralisation at Tönnersjöheden was similar to that observed at an adjacent Norway spruce site
454 (Persson and Nilsson, 2001). In addition, N deposition in this region is high (Bergholm et al., 2003),
455 resulting in plant inorganic N availability in the order of 10 g N m^{-2} yr^{-1}, i.e. 100 kg N ha^{-1}, which
456 enables high primary production. In contrast, net N mineralisation at Kivalo was very low, which is
457 typical of north boreal and tundra soils, where plants largely depend on uptake of organic N (Näsholm
458 et al., 2009). In addition, N deposition is much lower (Mustajärvi et al., 2008) than on the Swedish
459 west coast.
460
461 A number of conditions may have caused the higher nitrification rates in birch soil than pine and
462 spruce soils. Higher pH in combination with mixing of mineral soil and humus in birch soils were
463 probably the most important factors. There must also be NH_4^+ available for nitrifiers. It is possible that
464 the result reflects higher abundance and activity of nitrifying bacteria in birch soils under field
465 conditions. Nitrification under deciduous trees may be stimulated by enhanced soil ammonium levels
466 during winter, since the deciduous trees have a shorter growth period than evergreen conifers when
467 nitrate uptake can take place. The result of the present study agrees well with the observations by Ste-
468 Marie and Paré (1999) in Quebec, who compared soils of *Betula papyrifera*, *Picea glauca* and *Pinus*
469 *banksiana* stands, among others. However, there seems to be no general difference in nitrification
470 rates between deciduous and coniferous species. Trum et al. (2011) reported low nitrification rates in
471 soils of Norway spruce compared to high rates in Douglas-fir (*Pseudotsuga menziesii* Franco) soils,
472 and intermediate values in soils of oak (*Quercus petraea* (Matt.) Liebl.) and beech (*Fagus sylvatica*
473 L.).
474

The impact of tree species on the understorey vegetation was more pronounced at Tönnersjöheden than at Kivalo, as only mosses were present in the spruce plots, whereas the pine and birch plots had well-developed ground and field layer vegetation dominated by graminoids, forbs and dwarf shrubs. It is possible that the contribution of graminoid and forb litters in particular in the pine plots at Tönnersjöheden increased the C mineralisation rate compared with the spruce plots. In contrast, the mineralisation rate in the organic layer was significantly lower in pine plots than in spruce plots at Kivalo, where the ground layer vegetation differed, with the pine plots having the most dense moss layer, largely consisting of *Pleurozium schreberi* (Nieminen and Smolander, 2006). In spite of the fact that the understorey in pine plots at Tönnersjöheden was similar to that in birch plots, the abundance of earthworms was the same in pine as in spruce plots. This indicates that it was the birch litter rather than the understory vegetation that was the principal cause of the greater earthworm abundance in the birch plots.

The role of the understorey at Kivalo might have been somewhat different. Dwarf shrubs and mosses dominated, and they probably contributed to litter production at approximately equal rates. Moreover, Hilli et al. (2008) claimed that understorey vegetation contributes more to litter production in north boreal coniferous forests than in corresponding south boreal forests. Particularly moss litter could be expected to contribute more to SOM accumulation due to slower decomposition rates than e.g. *Vaccinium myrtillus* leaves. Under such conditions, tree species effects in the north boreal zone should generally be less marked than in the south boreal or temperate zones.

5. Conclusions

1. Tree species effects occurred mostly in the humus layer and were more pronounced at the temperate Tönnersjöheden site than at the north boreal Kivalo site, but there were also qualitative differences in tree species effects between sites.

2. Total field C heterotrophic respiration was greater in Norway spruce soil than in soils of Scots pine and silver birch plots at both sites, but the underlying causes were different. At the temperate site, higher field C mineralisation in spruce soil than in pine and birch soils was an effect of larger C pools in the humus layer of spruce, despite higher heterotrophic activity in birch soil than spruce soil. At the boreal site, higher field C mineralisation in spruce soil than in pine soil could be explained by lower heterotrophic activity in pine humus.

3. Typical north boreal characteristics were found at Kivalo, such as low C and N soil pools, high C/N ratios of SOM and low net N mineralisation rate.

4. At the temperate Tönnersjöheden site, the tree-species effects were manifested as differences between soils in conifer and birch plots. This was largely due to greater abundance of earthworms in the latter plots, which presumably caused a number of other changes such as higher pH, lower C/N ratio and higher proportion of nitrate in total N mineralisation.

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642 **Table 1**

643 Mean values of pH (H_2O) and C:N ratio in different soil layers at Tönnersjöheden and Kivalo.

644 Different letters indicate significant differences ($p<0.05$) between tree species.

645

	Tönnersjöheden			Kivalo		
	Silver birch	Scots pine	Norway spruce	Silver birch	Scots pine	Norway spruce
pH (H_2O)						
Humus layer	4.58 a	4.13 b	3.70 c	4.21	4.07	4.00
0–10 cm	4.41 a	4.12 b	4.01 b	4.77	4.51	4.59
10–20 cm	4.50	4.54	4.42	5.59	5.42	5.09
C:N ratio						
Humus layer	20.4 c	25.0 b	27.2 a	31.4 b	36.0 a	33.3 ab
0–10 cm	18.7 c	24.5 b	24.8 a	26.7	32.4	25.8
10–20 cm	20.1 b	22.0 a	22.9 a	24.3	27.7	26.9

646

647

648

Table 2

Mean accumulation rate of NH_4-N and NO_3-N (μg N g^{-1} C d^{-1}) at 15 °C in the humus layer (Oe + Oa) and the 0-10 and 10-20 cm mineral soil layers under different tree species at Tönnersjöheden in SW Sweden and Kivalo in N Finland (SE within parentheses). Different letters indicate significant differences ($p<0.05$) between tree species. Negative values indicate net immobilisation.

	Tönnersjöheden			Kivalo		
	Silver birch	Scots pine	Norway spruce	Silver birch	Scots pine	Norway spruce
NH_4-N						
Humus layer	29.7 (3.5) a	10.8 (1.6) b	9.1 (1.4) b	0.2 (0.3)	0.1 (0.0)	-1.0 (0.7)
0–10 cm	3.9 (4.6)	2.3 (1.6)	2.5 (0.9)	0.1 (0.1)	0.9 (0.6)	2.2 (1.7)
10–20 cm	1.0 (1.1)	1.1 (1.1)	0.3 (1.2)	0.8 (0.9)	0.3 (0.1)	1.1 (0.4)
NO_3-N						
Humus layer	4.9 (4.6) ab	4.9 (2.5) a	0.0 (0.0) b	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
0–10 cm	9.0 (4.6) a	3.0 (1.9) b	0.1 (0.1) b	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)
10–20 cm	6.2 (0.2)	2.3 (0.4)	1.9 (1.9)	0.6 (0.3)	0.0 (0.0)	0.7 (0.3)

Figure captions

Fig. 1. Mean C (above) and N (below) pools (± SE) in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil in stands of different tree species at Tönnersjöheden and Kivalo. Different upper-case and lower-case letters indicate significant differences ($p<0.05$) in total pools and pools of specific soil layers, respectively.

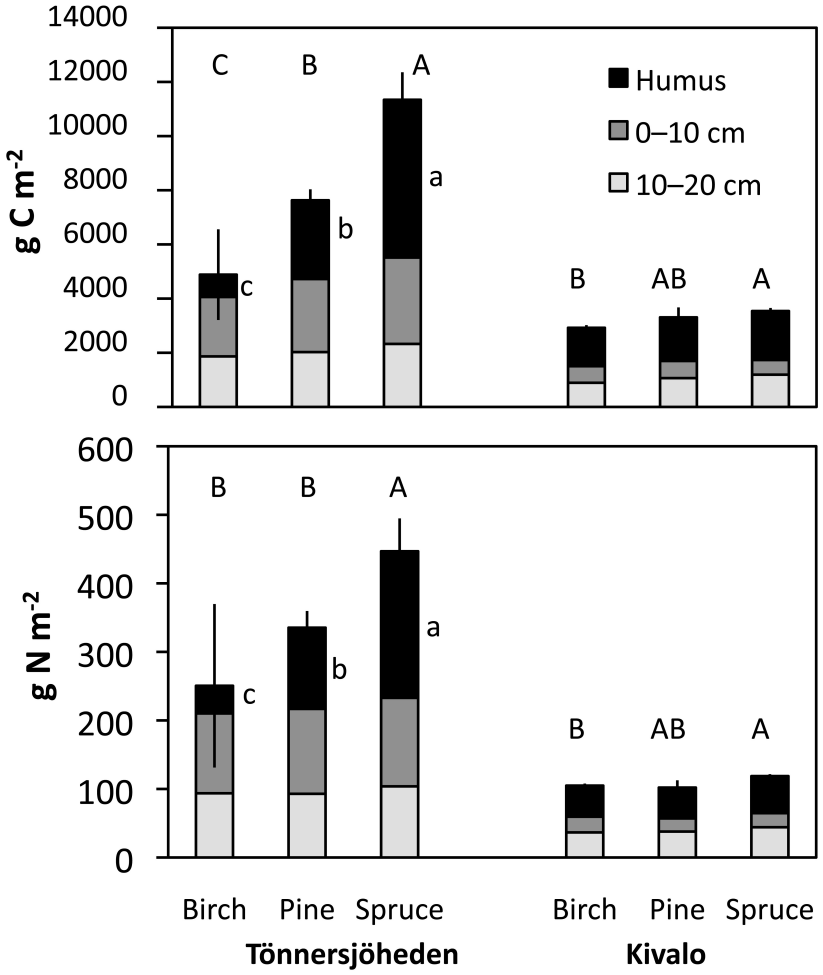
Fig. 2. Mean C mineralisation rate (± SE) at 15 °C in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil in stands of different tree species at Tönnersjöheden and Kivalo. Different letters indicate significant differences ($p<0.05$) between tree species.

Fig. 3. Mean net N mineralisation rates (± SE) at 15 °C in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil in stands of different tree species at Tönnersjöheden and Kivalo. Different letters indicate significant differences ($p<0.05$) between tree species.

Fig. 4. Estimated field annual C mineralisation (± SE) in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil in stands of different tree species at Tönnersjöheden and Kivalo. Different upper-case and lower-case letters indicate significant differences ($p<0.05$) in total C efflux and C fluxes from specific soil layers, respectively.

Fig. 5. Estimated field annual net N mineralisation (± SE) in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil in stands of different tree species at Tönnersjöheden and Kivalo (note difference in scales). Different upper-case and lower-case letters indicate significant differences ($p<0.05$) in total pools and pools of specific soil layers, respectively. The field estimates of ammonification and nitrification are approximate and

683 most likely under- and overestimates, respectively, because the nitrification rate was probably
684 favoured by the increase in ammonium concentration during the 30-day lab incubation.
685
686 **Fig. 6.** Mean abundance of earthworms (Lumbricidae) (± SE) in soil (Oi, Oe, Oa and mineral
687 soil 0-20 cm) in stands of different tree species at Tönnersjöheden.
688



689

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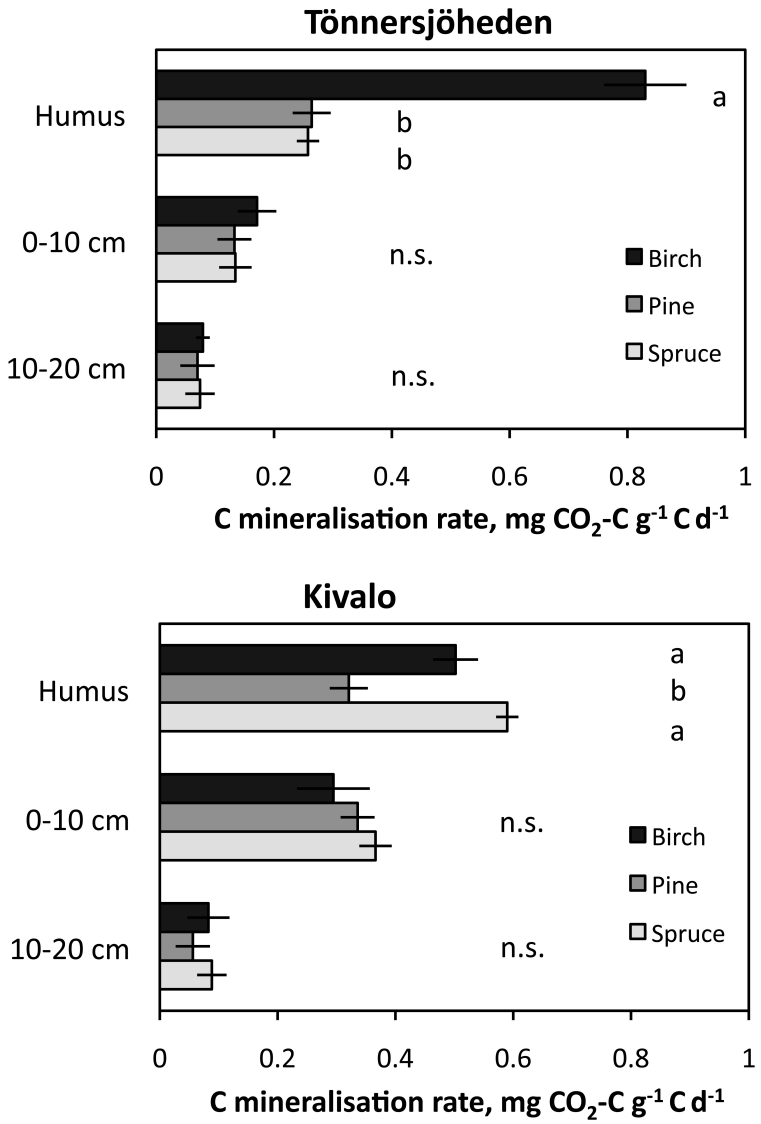
691 **Fig. 1.**

692



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694 **Fig. 2.**

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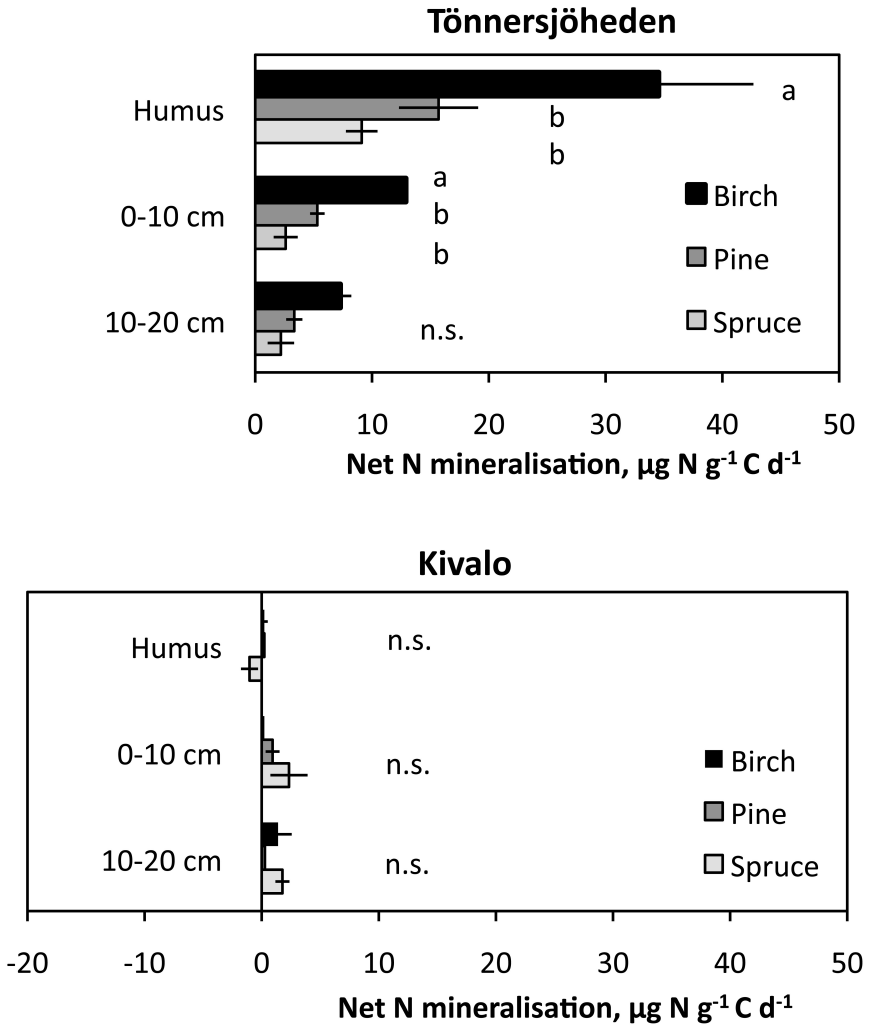

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698 **Fig. 3.**

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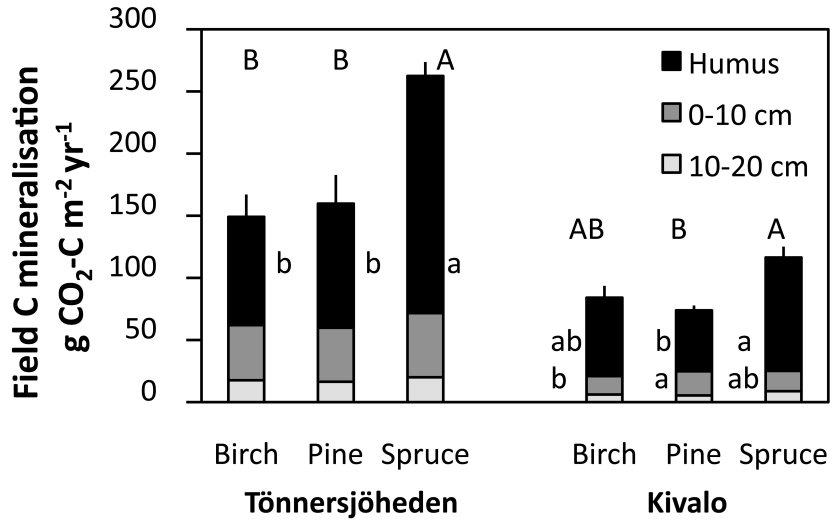

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701 **Fig. 4.**

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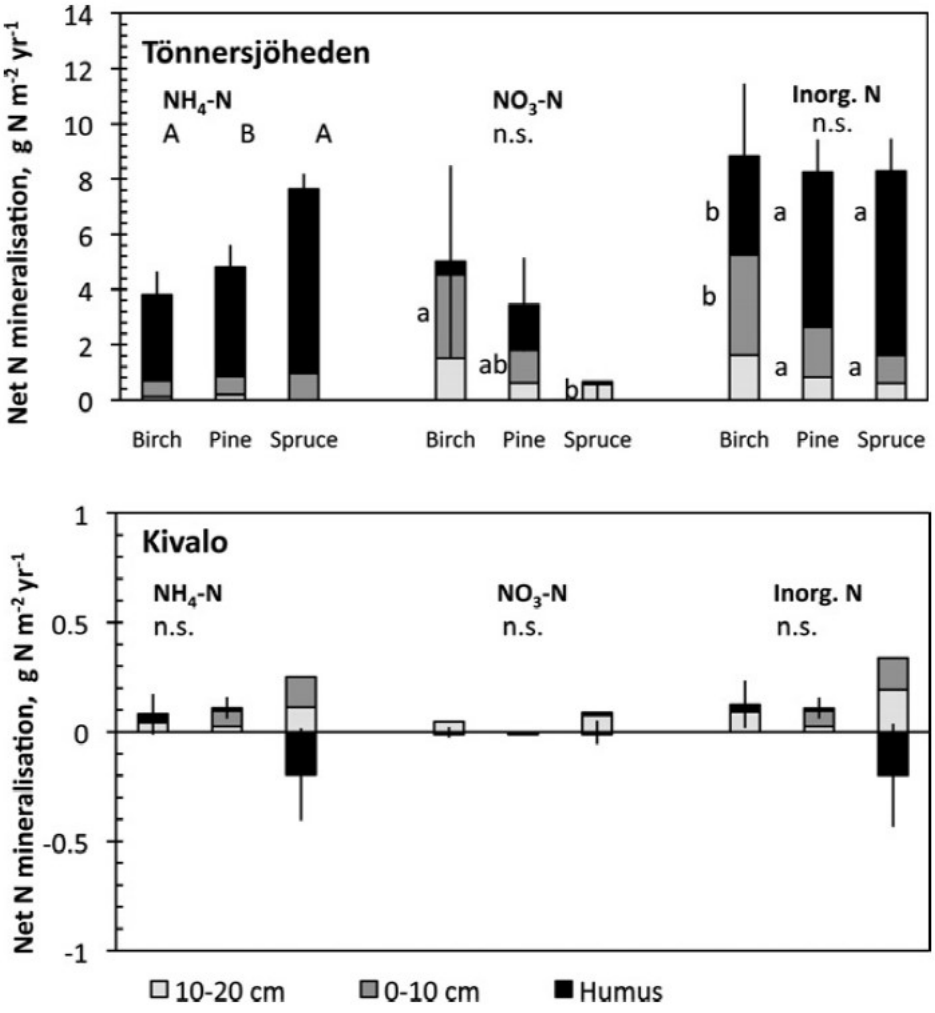

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705 **Fig. 5.**

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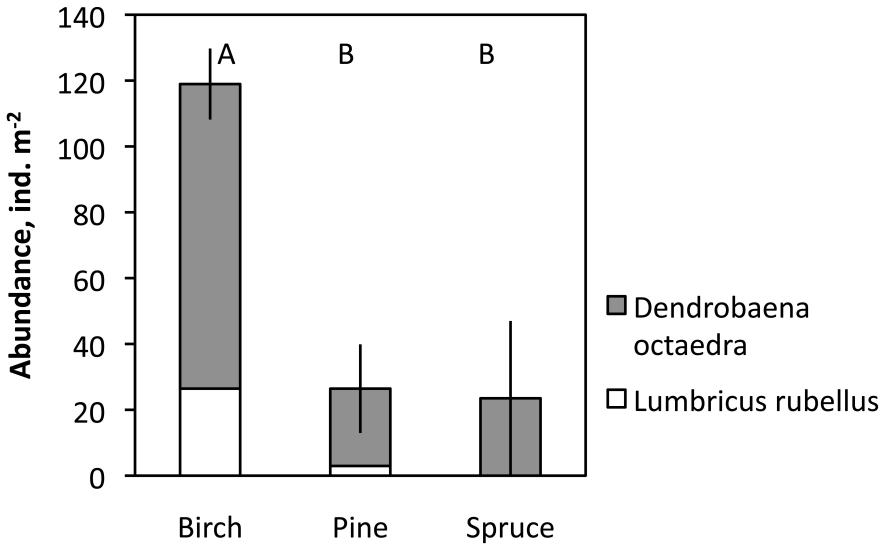

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709 **Fig. 6.**