Carbon and nitrogen pools and fluxes above and below ground in spruce, pine and birch stands in southern Sweden

Karna Hansson[a, 1, *], Mats Fröberg[b, 2], Heljä-Sisko Helmisaari[c], Dan B Kleja[b], Bengt A. Olsson[a], Mats Olsson[b], Tryggve Persson[a]

[a]*Department of Ecology, Box 7044, Swedish University of Agricultural Sciences, SE-75007 Uppsala, Sweden*

[b]*Department of Soil and Environment, Box 7014, Swedish University of Agricultural Sciences, SE-75007 Uppsala, Sweden*

[c]*Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland*

** Corresponding author. Tel. +33 383394077 ; Fax : +33 383394069*

[1]Present address: *Institut National de la Recherche Agronomique, UR 1138 Biogéochimie des Ecosystèmes Forestiers, 54280 Champenoux, France*

[2]Present address: *Department of Aquatic Sciences and Assessment, Box 7050, SE-750 07 Uppsala, Sweden*

E-mail addresses: karna.hansson@nancy.inra.fr (K Hansson); mats.froberg@slu.se (M Fröberg); helja-sisko.helmisaari@helsinki.fi (H-S Helmisaari), Dan.Berggren@slu.se (D B Kleja), Bengt.Olsson@slu.se (B Olsson), Mats.Olsson@slu.se (M Olsson),Tryggve.Persson@slu.se (T Persson)

Abstract

We synthesised results on soil carbon (C) and N fluxes and the accumulation of soil organic C and N under adjacent 50-yr-old Norway spruce, Scots pine and silver birch stands growing on similar soils and evaluated the different processes involved. C and N budgets were calculated. Spruce stands had larger stocks of C and N in biomass and soil than birch stands, with pine intermediate. The differences in soil stocks were mainly found in the organic layer, whereas differences in the mineral soil were small. The study showed that there is no simple answer to what is causing the differences in soil C and N stocks, because several processes are interacting. Spruce and pine trees had higher biomass and litter production than birch trees, but total litter inputs showed no significant difference between stands, because the rich ground vegetation under pine and birch contributed with substantial litter inputs, in contrast to the poor ground vegetation under spruce.
Decomposition rate (per g of C) was markedly higher under birch than under spruce and pine resulting in lower C and N stocks in the organic layer. This effect was amplified by higher abundance and biomass of earthworms, favoured by higher pH and palatable litter under birch. Earthworm bioturbation probably both increased decomposition rate and damaged the ectomycorrhizal network with negative consequences for the formation of mycorrhizal litter and C storage. In conclusion, the direct effects of spruce, pine and birch litter on C and N pools and fluxes were modified by indirect effects on understorey structure, pH and earthworm responses.

Keywords: *Pinus sylvestris, Picea abies, Betula pendula*, carbon, nitrogen, soil

1. Introduction

Carbon (C) sequestration in forest soils have been the focus of many scientific studies in the last 25 years, both globally and for different forest ecosystems (e.g. Vogt, 1991; Dixon et al., 1994; Ågren et al., 2007; Ciais et al., 2008; Olsson et al., 2009; Nouvellon et al., 2012; Gamfeldt et al., 2013). Tree species are known to influence soil properties (Binkley and Giardina, 1998; Augusto et al., 2002; Stendahl et al., 2010), but only a few studies (e.g. Vesterdal et al., 2008; Calvaruso et al., 2011) have been able to separate the effects of tree species on soil properties from the confounding effects of soil properties on stand type . In Sweden, Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *B. pubescens*) are the dominating tree species, together representing more than 90 % of standing forest volume (Anonymous, 2011). Reforestation after harvest is common practice in Swedish forest management, and spruce is generally preferred over pine on mesic, high quality sites. Birch does not typically occur in pure stands. Thus forest management also significantly affects the abundance of tree species in Swedish forests.

Several attempts have been made to quantify C sequestration for different species at the national level in Sweden based on different approaches and data sources. Ågren et al. (2007) combined national forestry statistics (1926–2000), allometric biomass functions and a model of litter decomposition to estimate Swedish forest soil C sinks and sources. They found that Norway spruce stands generally had larger C stocks than stands of Scots pine. This result was essentially an effect of the higher biomass production in spruce stands, particularly of needle and fine-root litters. Stendahl et al. (2010) found similar differences in soil C stocks between the two species from analyses of Swedish National Forest Soil Inventory data. The national average soil organic C stock was 9.2 kg m^{-2} in spruce-dominated stands and 5.7 kg m^{-2} in pine-dominated stands. In addition, a simulation of C dynamics in different stand types revealed 24% higher biomass production in spruce than in pine stands during a single rotation period when grown under identical site conditions, but litter production rates were higher for most biomass components in pine stands, and there was also a greater contribution of litters from ground vegetation in pine stands. Akselsson et al. (2005) modelled C sequestration in the organic layers of Swedish forest soils, based on the relationship between the actual evapotranspiration and litter production of different tree species, in combination with the limit value of litter decomposition for each species. On average, Norway spruce stands annually accumulated 200 kg C ha^{-1} whereas Scots pine and birch stands accumulated 150 kg C ha^{-1} yr^{-1}. Gamfäldt et al. (2013) used Swedish National Forest Inventory data and analysed effects of tree species diversity on multiple ecosystem services, among them soil C sequestration. They found that soil carbon storage increased with tree species richness and (among the species included in the study), biomasses of birch and spruce were positively related to soil C storage. Thus, these studies support that Norway spruce produces higher soil C stock than Scots pine (and birch), although the mechanisms behind differed or were not clearly distinguished.

The general picture of tree species effects on soil C stocks (silver birch < Scots pine < Norway spruce) based on Swedish regional empirical studies and simulations is supported by experimental tests in other regions. For example, Mueller et al. (2012) found that Norway spruce had, on average, higher soil C pools than silver birch and Scots pine after 30 yrs in the Siemianice Experimental Forest in Poland. In a 30-yr-old common garden experiment in Denmark, Vesterdal et al. (2008; 2012) observed that Norway spruce had much higher C contents in the forest floor than ash, lime, maple, oak and beech (birch not included), but the differences were not significant when viewed for the whole soil profile. In contrast to these results, Frouz et al. (2009) reported accumulation of soil organic C in the order natural regeneration (including birch) < spruce < pine, oak < larch < alder < lime on 22-32-yr-old post-mining sites in the Czech Republic. However, the soil at these sites (tertiary clay) had a pH of 8, which is too high for optimal growth of pine (Ellenberg, 1986).

To separate tree species effects from other site differences, such as soil parent material, we compared C stocks and dynamics in stands of spruce, pine and birch, at an experimental site in the cold temperate zone in south-west Sweden, using a block design. Ground vegetation, depth of humus layer, earthworm abundance and top soil pH significantly differed among the species (Table 1). Birch stands had more developed ground vegetation, thinner humus layers, more and larger earthworms and higher pH than spruce stands, with pine intermediate (Hansson et al., 2011; Olsson et al., 2012). Amounts of exchangeable base cations (K, Ca, Mg and Na) differed among the tree species in the humus layer, but not in the mineral soil, with the largest amounts in the spruce stands and smallest in birch stands (Hansson et al., 2011). C and N fluxes and the accumulation of soil organic C differ between tree species at this site. Results of these studies have been presented in earlier papers (Fröberg et al., 2011a; Hansson et al., 2011; Olsson et al., 2012; Hansson et al., 2013 this issue). Here, we synthesise the main results of this comparison of birch, pine and spruce stands in southern Sweden. We present soil C and N budgets and evaluate the major processes controlling soil C and N pools and fluxes in these forests.

2. Materials and methods

2.1 Study site

The Tönnersjöheden Experimental Forest is located in south-west Sweden (56°40-41'N, 13°03-06'E), at an elevation of 70-90 m above sea level. Mean annual air temperature is 6.4 °C and mean annual precipitation is 1053 mm. Length of the growing season (>5 °C) is 204 days. The experimental design included stands of three tree species, Norway spruce (*Picea abies* (L) Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth), replicated in a block design (n=3, except for birch where n=2). Similarly aged stands with different stand density were selected, reflecting the situation in the region, with spruce often having larger basal area per hectare than birch. This enabled comparison of differences caused not only by species *per se*, but also by differences in e.g. ground vegetation following the different light conditions in the stands, rather than comparing stands with similar basal area. In 1890, blocks 1 and 2 in the present study area were heather moorland with admixture of pine and birch, whereas block 3 was a sparse birch forest with admixture of pine. By 1930, blocks 1 and 2 consisted of dense stands of Norway spruce with admixture of Scots pine, whereas silver birch dominated in block 3. The present stands in the study area were established in 1951-1963.

The soil parent material is sandy or loamy sand and of glacifluvial origin, and the soils show signs of podzolisation, but are weakly developed and may be classified as podzols, arenosols or regosols. There were no significant differences in soil type, texture or geochemistry between stands of different species (Table 2), confirming that the experimental plots have similar background. More details about the study site can be found in Hansson et al. (2011).

2.2 Budget estimates

C and N pools and fluxes, illustrated in Figs. 1 and 2, and C and N budgets (input = accumulation + losses) were estimated (data sources presented in Table 3). C and N inputs included estimates of aboveground litterfall (trees, shrubs and ground vegetation) and below ground litter (fine roots) (Hansson et al., 2013 this issue).
C and N soil stocks in humus layer and 0-30 cm depth in mineral soil were measured (Hansson et al., 2011). C losses were estimated as heterotrophic respiration (R_H) (Olsson et al., 2012) and DOC (Fröberg et al., 2011a). N losses from the soil were estimated as leaching of dissolved N [DN=dissolved organic N (DON) + dissolved inorganic N (DIN)] (Fröberg et al., 2011a) and recirculation of N through net N mineralisation (Olsson et al., 2012).

Data on C pools at stand establishment are lacking. For budget calculations, we assumed that the soil C pool in pine, with intermediate C stocks, remained unchanged since plantation and, thus, represents the starting baseline for all stands. We assumed same C stocks in all stands at stand establishment, based on similar soil texture and geochemistry (Table 2) as well as similar soil history before stand establishment.

Tree basal area (Hansson et al., 2011) and height of the different stands were measured in 2009-2010 and aboveground and belowground biomass were calculated using correlation functions from the literature (Table 4). C content was estimated as 50% of biomass.

Understorey vegetation consisted of ground vegetation, shrubs and trees other than the dominant tree species layer, including large trees of species other than the dominant species and also small trees of the dominant species. The ground vegetation layer was defined as vegetation <50 cm height, and the shrub layer as vegetation >50 cm height. Litter input from the ground vegetation layer was calculated as biomass (Hansson et al., 2011) divided by estimated longevity (Table 5).

For ericoid dwarf shrubs, leaf biomass was assumed to be 25% of total biomass (Parsons et al., 1994). The spruce plots had no shrub layer vegetation, whereas small trees and shrubs were common in the pine and birch stands. To determine shrub layer aboveground biomass, five circular subplots (diameter 9 m) were selected in each pine and birch plot. Within each circle, height and diameter of each tree/shrub were measured (at root collar and, when applicable, at breast height, 130 cm). Aboveground biomass was estimated using correlations between diameter, height, volume and biomass. For most species these correlation functions were taken from the literature (Table 6), but for *Frangula alnus,* 10 shrubs of different sizes were harvested and a correlation function calculated. For some species the correlation was assumed to be the same as for other, similar species (Table 6).

Litterfall from understorey trees was calculated using correlations between diameter, height and leaf biomass. For most species correlation functions were taken from the literature (Table 6), but for some species leaf biomass was simply assumed to be 1% of total biomass. This estimate is lower than allometric functions typically suggest, but is justified by the fact that suppressed trees often have low leaf biomass in relation to woody components (B. Olsson unpublished data). Leaf longevity was estimated to be 6 years for spruce and 1 year for other species. C content was estimated as 50% of biomass. N content was estimated using literature data (Tables 5 and 6).

In this study, no N deposition estimates were carried out, and for the budget estimates, we adopted the rough figures presented by Karlsson et al. (2010). They estimated throughfall in spruce, pine and deciduous stands to be about 1.5, 1.0 and 1.0 g m^{-2} yr^{-1} in south-western Sweden. Because throughfall was generally higher than bulk deposition, we considered that net canopy interception of N was negligible and that all N deposition reached the soil system as NH_4-N and NO_3-N.

Mean residence time (MRT, years) of the soil C stocks in different soil layers was estimated as the quotient between the C pool (g C m^{-2}) and heterotrophic respiration [R_H, g CO_2-C (g C)$^{-1}$ yr^{-1}] in each soil layer.

3. Results and discussion

3.1 C and N pools

Tree standing biomass, soil C and N stocks, and C and N fluxes differed among the three tree species in these 50-year-old stands. Total plant biomass C was estimated at 6.0, 8.6 and 11.5 kg m^{-2} in birch, pine and spruce stands, respectively (Fig. 1).

Differences in soil C and N stocks between spruce and birch were about 3 kg C and 0.1 kg N m^{-2} (Figs. 1 and 2). These differences, which had accumulated since the establishment of the experimental plots 50 years earlier, correspond to mean differences in fluxes of about 60 g C m^{-2} yr^{-1} and 2 g N m^{-2} yr^{-1}. The differences in soil C and N stocks between spruce and pine at the time of sampling amounted at 2.3 kg C and 0.08 kg N m^{-2}. These differences in stocks correspond to differences in fluxes of about 47 g C m^{-2} yr^{-1} and 1.6 g N m^{-2} yr^{-1}. The difference in soil C stocks between spruce and pine stands is lower than (but on the same order of magnitude as) the average difference (3.5 kg C m^{-2}) according to the Swedish National Forest Soil Inventory (Stendahl et al., 2010).

3.2 Litter inputs

Total aboveground litterfall (including understorey), did not significantly differ between tree species, but litterfall from trees during 2007-2010 was significantly higher in pine (137 g C m^{-2} yr^{-1}) and spruce (128 g C m^{-2} yr^{-1}) stands than in birch stands (72 g C m^{-2} yr^{-1}) (Hansson et al., 2011). Estimated litterfall from shrubs and ground vegetation was higher in birch (84 g C m^{-2} yr^{-1}) and pine stands (71 g C m^{-2} yr^{-1}) than in spruce stands (24 g C m^{-2} yr^{-1}). However, these data on litterfall cover only a minor part of the 50 years of stand development. The large species differences in tree biomass suggest that relative differences in litter inputs between stands may previously have been higher. The difference in understorey litter input is consistent with results from other studies. Alriksson and Eriksson (1998) report lower field vegetation biomass in spruce stands than in pine and birch stands. In pine, spruce and birch stands in northern Finland, Smolander and Kitunen (2002) found more herbs and grasses in the birch stands than in the coniferous stands. The low understorey litter production in the spruce stands can be explained by the denser canopy and poorer light conditions for shrubs and ground vegetation. Leaf area index, measured at 2 m height, was 1.3 (birch), 2.2 (pine) and 4.2 (spruce). Spruce understorey was dominated by mosses with an estimated longevity of 5 years, compared with 1-1.5 years for grasses, forbs and ericoid dwarf shrubs common in the pine and birch stands (Table 5).

Fine root litter inputs were estimated to be highest in spruce stands (130 g C m^{-2} yr^{-1}) followed by pine (106 g C m^{-2} yr^{-1}) and birch (77 g C m^{-2} yr^{-1}) stands (Hansson et al., 2013 this issue). The belowground inputs thus reflect the higher biomass in the spruce.

Total C inputs in foliar and root litters were estimated at 233, 314 and 282 g C m^{-2} yr^{-1} in the birch, pine and spruce stands, respectively, for the period 2007- 2010. Total inputs of organic N in above and below ground litter fractions were 7.7, 8.3 and 7.7 g N m^{-2} yr^{-1} in birch, pine and spruce stands, respectively (Fig. 2). The lower total C litter inputs in the birch stands compared with pine and spruce suggests that differences in litter inputs contributed significantly to the observed differences in soil C stocks, but there was no difference in litter inputs between the pine and spruce stands. Spruce stands had a larger portion of fine-root litter in the total litter production. This observation is in line with the national-scale predictions by Ågren et al. (2007) that fine-root turnover had a more marked influence on C sequestration in spruce than in pine forests.

3.3 C and N losses

Although there were statistically significant differences in DOC leaching between tree species (Fröberg et al., 2011a), these losses were small and not quantitatively important for the ecosystem budget (Fig. 1). DOC fluxes are generally small compared with other ecosystem fluxes, and while DOC loss can be important for redistribution of C within the soil profile, net DOC leaching from the soil usually does not constitute a major loss of C (Michalzik et al., 2001). Differences among tree species in C losses are therefore related to CO_2.

Estimated total (humus and 0-20 cm mineral soil) annual C mineralisation was significantly higher in spruce plots than in pine and birch plots. This difference is the result of the significantly larger C pool in the humus layer despite the relatively low C mineralisation rate in spruce plots. The low decomposition rate in coniferous stands is consistent with data from Denmark, where lower annual C losses (Vesterdal et al., 2008) and lower turnover rates (Vesterdal et al., 2012) have been reported in spruce stands compared with broad-leaf species. Likewise, Priha et al. (2001) reported higher C mineralisation rates in birch than in spruce stands in Finland, with pine intermediate.

While there were negligible effects of tree species on DOC leaching, this was not the case for total N leaching. Losses of DN from under the B horizon were lower in the spruce stands (0.2 g m^{-2} yr^{-1}) than in pine (0.7 g m^{-2} yr^{-1}) or birch (0.9 g m^{-2} yr^{-1}) stands, which may be attributable to the larger capacity of the fast-growing spruce stand to take up N from the soil solution (Fröberg et al., 2011a).

Estimated total (humus and 0-20 cm mineral soil) net N mineralisation was about 8 g N m^{-2} yr^{-1}, but there was no significant difference among tree species (Fig. 2) (Olsson et al., 2012). It could be expected that the higher N deposition in coniferous stands could result in higher N leaching (Tipping et al., 2012), but this was not the case in our study. The lower N leaching in spruce compared with birch stands (Fig. 2) may be the result of the faster-growing spruce stands taking up more N.

3.4 C budgets

The influx of C in litter components was higher in pine and spruce than in birch stands, whereas R_H was higher in spruce than in pine and birch stands, and DOC flux was higher in pine than in spruce stands, with birch intermediate (Fig. 1). The accumulation of soil C was greater in spruce than in pine and birch stands assuming equal amounts of soil C at the start of the experiment 50 years before soil sampling. If we assume that the soil C pool in pine stands remained unchanged since planting and, thus, represents the starting baseline for all stands, the increase in soil C in spruce would on average be 47 g C m^{-2} yr^{-1} and the budget would be 282 (litter input) = 47 (accumulation) + 270 (R_H) + 3 (DOC) g C m^{-2} yr^{-1}.

Fig. 1 shows only the measured variables, and does not contain estimates of (1) coarse woody debris (CWD), (2) extramatrical mycorrhizal litter and (3) R_H from the Oi layer, which all can affect the C budget considerably. Stumps are the largest CWD component in managed forests, and Palviainen et al. (2010) reported significantly faster C and N losses from birch stumps than from pine and spruce stumps during decomposition. However, 50-yr-old stumps are to a large extent decomposed (Palviainen et al., 2010) and so should not have contributed much to litter input in our study.

The input of extramatrical mycorrhizal litter is difficult to estimate but probably significant. Recent data on ^{13}C signatures in deep humus layers indicate high contribution from mycorrhizal litter (Clemmensen et al., 2013). We assumed extramatrical mycorrhizal litter to amount to 10% of fine-root litter, in agreement with data from the nearby site Skogaby (Nilsson and Persson, 2001), and the C and N concentrations in the hyphae were assumed to be 45% and 3%, respectively (C/N=15).

Heterotrophic respiration from the O_i layer was not estimated in our study, but was found to be 64 g CO_2-C m^{-2} yr^{-1} in a nearby 40-yr-old spruce stand (Skogaby) and corresponded to an amount of 40% of the above-ground litterfall (T. Persson, pers. comm.). Assuming the same relations in our study,

R_H from the O_i layer amounted at 62, 83 and 61 g C m^{-2} yr^{-1} in birch, pine and spruce stands, respectively.

When both measured and deduced fluxes were taken into consideration, an adjusted C budget was constructed (Table 7). This budget shows that estimated litter input is higher than R_H/DOC outputs for birch (13%) and pine (21%), whereas the input is lower than output for spruce (29%). A totally balanced budget was not expected, as the accumulation of soil C is a function of all litter inputs during 50 years, whereas the estimates of C fluxes were based on estimates at the end of this period.

3.5 N budgets

The ecosystem N budget includes N deposition as input and dissolved N as output; gaseous N losses were not measured. Estimated losses of dissolved N as DIN and DON were 0.9, 0.7 and 0.2 g N m^{-2} yr^{-1} in birch, pine and spruce, respectively (Fig. 2). This indicates that in birch and pine, a similar amount of N as enters in throughfall (Karlsson et al., 2010) (about 1 g N m^{-2} yr^{-1}) leaches out of the system. In contrast, in spruce, only a small fraction of the N deposited in throughfall (about 1.5 g N m^{-2} yr^{-1}) is lost from the ecosystem (Table 8). The "external" N balance in Table 8, thus, shows what can be utilized by plant uptake. However, this uptake is only a small fraction of total uptake, because the internal turnover of N released mineralised N (8.2-8.8 g N m^{-2} yr^{-1}) (Fig. 2). Consequently, plant uptake of N (deposition + net N mineralisation – leaching) is estimated to be 8.9, 8.5 and 9.5 g N m^{-2} yr^{-1} for birch, pine and spruce (Table 8). The higher uptake of N in spruce can partly explain higher N pools (not measured but deduced from high needle mass) in spruce biomass, but could not be demonstrated to be re-circulated as litter N.

The "internal" N budget showed that soil N pools differed between tree species in similar proportions as for the C pools (Fig. 2). Estimated litter inputs (7.7-8.3 g N m^{-2} yr^{-1}) and outputs in the form of net N mineralisation were reasonably well balanced. However, the N pools under spruce showed an accumulation of 1.6 g N m^{-2} yr^{-1} over the 50 experimental years in relation to pine. When the input of external mycorrhizal litter N was not included (see below), the input of 7.7 g N m^{-2} yr^{-1} was lower than the sum net N mineralisation (8.3 g N m^{-2} yr^{-1}) and soil N accumulation (1.6 g N m^{-2} yr^{-1}).

As with the C budget, extramatrical mycorrhizal litter and net N mineralisation in the Oi layer were not measured. The extramatrical mycorrhizal litter was assumed to have relatively high N concentration (3%) and could, thus, contribute substantially to total litter input (Table 9). Net N mineralisation was assumed to be 0 in the O_i layer. This assumption is based on relatively high C/N ratios in litterfall, 28, 37 and 35 in birch, pine and spruce, respectively.

The internal N budget is summarised in Table 9, which shows that the N balance was positive (greater inputs, +9%) in pine and negative (greater outputs/accumulation, -14%) in spruce. In birch stands, the inputs and outputs were almost balanced.

3.6C Mean residence time (MRT)

Differences in soil C and N stocks occurred primarily in the O horizon, whereas differences in stocks in the mineral soil were small and statistically non-significant (Hansson et al., 2011). In the O horizon the MRT of C is generally shorter (about 30-40 years; Fröberg et al., 2011b) than the current stand age of approximately 50-60 years and most of the organic matter in this horizon was therefore probably derived from the current stand. Estimated MRT in the Oe+Oa horizon (Table 10) ranged from 9.5 years (birch) to 31 years (spruce). The remarkably short MRT (and high respiration rate) in the birch stands is related to the higher pH and much higher populations of earthworms than in the other stands (Olsson et al., 2012). In areas where earthworms have historically been absent, introduction of earthworms have stimulated the microbial activity (Li et al., 2002), reduced or eliminated the organic layer, increased the ratio of bacteria to fungi (Dempsey et al., 2011), and decreased colonisation rates and total abundance of AM mycorrhiza on sugar maple roots

(Lawrence *et al.*, 2003). In a common garden experiment with Norway spruce, red oak and sugar maple, Melvin and Goodale (2013) found that forest floor MRT correlated negatively with earthworm density and did not correlate with any measurement of litter chemistry. On the other hand, earthworm density correlated well with soil pH, being lower in spruce than in maple and oak. These and our findings suggest that tree species have both direct (litter quality and quantity) and indirect (pH and earthworm responses) effects on soil C and N turnover. The generally small and statistically non-significant differences in C pools in the mineral soil are in accordance with longer turnover times for organic matter and therefore slow changes in this pool. Estimated MRT was 140-205 years at 20-30 cm depth in the mineral soil (Table 10).

3.7 Conclusions

The comparison of 50-year-old stands of silver birch, Scots pine and Norway spruce showed that C and N pools in both soil and standing biomass were higher in spruce than in birch plots, with pine intermediate. Species differences in C and N stocks in soil were mainly found in the organic layer, whereas differences in the mineral soil were small. The study also showed that there is no simple answer to what is causing the differences in soil C and N stocks, because several processes are interacting. Spruce and pine trees had higher biomass and litter production than birch trees, but total litter inputs showed no significant difference between stands, because the rich ground vegetation under pine and birch contributed with substantial litter inputs, in contrast to the poor ground vegetation under spruce. Decomposition rate (per g of C) was markedly higher under birch than under spruce and pine resulting in lower C and N stocks in the organic layer. This effect was amplified by higher abundance of earthworms, favoured by higher pH and palatable litter under birch. Earthworm bioturbation probably both increased decomposition rate and damaged the ectomycorrhizal network with negative consequences for the formation of mycorrhizal litter and C storage. In conclusion, the direct effects of spruce, pine and birch litter on C and N pools and fluxes were modified by indirect effects on understorey structure, pH and earthworm responses.

Acknowledgements

The study was originally initiated by Professor Hooshang Majdi, deceased 2007. The research was supported by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning.

References

Ågren, G., Hyvönen, R., Nilsson, T., 2007. Are Swedish forest soils sinks or sources for CO_2—model analyses based on forest inventory data. Biogeochemistry 82, 217-227.

Akselsson, C., Berg, B., Meentemeyer, V., Westling, O., 2005. Carbon sequestration rates in organic layers of boreal and temperate forest - Sweden as a case study. Global Ecology and Biogeography 14, 77-84.

Alriksson, A., Eriksson, H.M., 1998. Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. For. Ecol. Manage. 108, 261-273.

Anonymous, 2011. Skogsdata 2011. Aktuella uppgifter om de svenska skogarna från riksskogstaxeringen. Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59, 233-253.

Bartelink, H.H., 1997. Allometric relationships for biomass and leaf area of beech (*Fagus sylvatica* L). Ann. For. Sci. 54, 39-50.

Binkley, D., Giardina, C., 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42, 89-106.

Calvaruso, C., N'Dira, V., Turpault, M.-P., 2011. Impact of common European tree species and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) on the physicochemical properties of the rhizosphere. Plant Soil 342, 469-480.

Ciais, P., Schelhaas, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J., Luyssaert, S., Le-Maire, G., Schulze, E.D., Bouriaud, O., Freibauer, A., Valentini, R., Nabuurs, G.J., 2008. Carbon accumulation in European forests. Nature Geosci 1, 425-429.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and Associated Fungi Drive Long-Term Carbon Sequestration in Boreal Forest. Science 339, 1615-1618.

Dempsey, M.A., Fisk, M.C., Fahey, T.J., 2011. Earthworms increase the ratio of bacteria to fungi in northern hardwood forest soils, primarily by eliminating the organic horizon. Soil Biol. Biochem. 43, 2135-2141.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., Wisniewski, J., 1994. Carbon Pools and Flux of Global Forest Ecosystems. Science 263, 185-190.

Ellenberg, H., 1986. Lebensbereiche der wichtigen baumarten. In, Vegetation mitteleuropas mit den Alpen. Ulmer, Stuttgart, pp. 79-86.

Fröberg, M., Hansson, K., Kleja, D.B., Alavi, G., 2011a. Dissolved organic carbon and nitrogen leaching from Scots pine, Norway spruce and silver birch stands in southern Sweden. For. Ecol. Manage. 262, 1742-1747.

Fröberg, M., Tipping, E., Stendahl, J., Clarke, N., Bryant, C., 2011b. Mean residence time of O horizon carbon along a climatic gradient in Scandinavia estimated by ^{14}C measurements of archived soils. Biogeochemistry 104, 227-236.

Frouz, J., Pižl, V., Cienciala, E., Kalčík, J., 2009. Carbon storage in post-mining forest soil, the role of tree biomass and soil bioturbation. Biogeochemistry 94, 111-121.

Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusinski, G., Andersson, E., Westerlund, B., Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340 DOI:1310.1038/ncomms2328.

Hamburg, S., Zamolodchikov, D., Korovin, G., Nefedjev, V., Utkin, A., Gulbe, J., Gulbe, T., 1997. Estimating the carbon content of russian forests; A comparison of phytomass/volume and allometric projections. Mitigation and Adaptation Strategies for Global Change 2, 247-265.

Hansson, K., Helmisaari, H., Sah, S., Lange, H., 2013 this issue. Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. For. Ecol. Manage.

Hansson, K., Olsson, B.A., Olsson, M., Johansson, U., Kleja, D.B., 2011. Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden. For. Ecol. Manage. 262, 522-530.

Johansson, T., 1999. Biomass equations for determining fractions of pendula and pubescent birches growing on abandoned farmland and some practical implications. Biomass Bioenerg. 16, 223-238.

Karlsson, G., Akselsson, C., Hellsten, S., Karlsson, P., Malm, G., 2010. Övervakning av Luftföroreningar i Hallands Län–Mätningar och Modellering. In, IVL Rapport. Swedish Environmental Research Institute, pp. 1-41.

Karlsson, P.S., 1992. Leaf longevity in evergreen shrubs: variation within and among European species. Oecologia 91, 346-349.

Konôpka, B., Pajtík, J., Moravcík, M., Lukac, M., 2010. Biomass partitioning and growth efficiency in four naturally regenerated forest tree species. Basic and Appl. Ecol. 11, 234-243.

Lawrence, B., Fisk, M.C., Fahey, T.J., Suárez, E.R., 2003. Influence of nonnative earthworms on mycorrhizal colonization of sugar maple (*Acer saccharum*). New Phytol. 157, 145-153.

Li, X., Fisk, M.C., Fahey, T.J., Bohlen, P.J., 2002. Influence of earthworm invasion on soil microbial biomass and activity in a northern hardwood forest. Soil Biol. Biochem. 34, 1929-1937.

Marklund, L.G., 1988. Biomassafunktioner för tall, gran och björk i Sverige. Biomass functions for pine, spruce and birch in Sweden. In. Swedish University of Agricultural Sciences, Umeå, pp. 1-73.

Melvin, A.M., Goodale, C.L., 2013. Tree species and earthworm effects on soil nutrient distribution and turnover in a northeastern United States common garden. Can. J. For. Res. 43, 180-187.

Michalzik, B., Kalbitz, K., Park, J.H., Solinger, S., Matzner, E., 2001. Fluxes and concentrations of dissolved organic carbon and nitrogen – a synthesis for temperate forests. Biogeochemistry 52, 173-205.

Mueller, K., Eissenstat, D., Hobbie, S., Oleksyn, J., Jagodzinski, A., Reich, P., Chadwick, O., Chorover, J., 2012. Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment. Biogeochemistry DOI 10.1007/s10533-011-9695-7, 1-14.

Nilsson, L., Persson, T., 2001. The Skogaby experiment-effect of N and S deposition to a forest ecosystem. In, Naturvårdsverket Report. Swedish Environmental Protection Agency, Stockholm.

Nouvellon, Y., Laclau, J.-P., Epron, D., Le Maire, G., Bonnefond, J.-M., Gonçalves, J.L.M., Bouillet, J.-P., 2012. Production and carbon allocation in monocultures and mixed-species plantations of Eucalyptus grandis and Acacia mangium in Brazil. Tree Physiology 32, 680-695.

Økland, R.H., 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. J. Ecology 83, 697-712.

Olsson, B.A., Hansson, K., Persson, T., Beuker, E., Helmisaari, H.-S., 2012. Heterotrophic respiration and nitrogen mineralisation in soils of Norway spruce, Scots pine and silver birch stands in contrasting climates. For. Ecol. Manage. 269, 197-205.

Olsson, M.T., Erlandsson, M., Lundin, L., Nilsson, T., Nilsson, Å., Stendahl, J., 2009. Organic carbon stocks in Swedish podzol soils in relation to soil hydrology and other site characteristics. Silva Fenn. 43, 209-222.

Palviainen, M., Finér, L., Laiho, R., Shorohova, E., Kapitsa, E., Vanha-Majamaa, I., 2010. Carbon and nitrogen release from decomposing Scots pine, Norway spruce and silver birch stumps. For. Ecol. Manage. 259, 390-398.

Parsons, A., Welker, J., Wookey, P., Press, M., Callaghan, T., Lee, J., 1994. Growth responses of four sub-Arctic dwarf shrubs to simulated environmental change. J. Ecology, 307-318.

Priha, O., Grayston, S.J., Hiukka, R., Pennanen, T., Smolander, A., 2001. Microbial community structure and characteristics of the organic matter in soils under Pinus sylvestris, Picea abies and Betula pendula at two forest sites. Biol. Fertil. Soils 33, 17-24.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proc. Natl. Acad. Sci. USA 101, 11001-11006.

Repola, J., 2008. Biomass equations for birch in Finland. Silva Fenn. 42, 605-624.

Smolander, A., Kitunen, V., 2002. Soil microbial activities and characteristics of dissolved organic C and N in relation to tree species. Soil Biology and Biochemistry 34, 651-660.

Stendahl, J., Johansson, M.B., Eriksson, E., Nilsson, Å., Langvall, O., 2010. Soil organic carbon in Swedish spruce and pine forests - Differences in stock levels and regional patterns. Silva Fenn. 44, 5-21.

Tipping, E., Rowe, E.C., Evans, C.D., Mills, R.T.E., Emmett, B.A., Chaplow, J.S., Hall, J.R., 2012. N14C: A plant–soil nitrogen and carbon cycling model to simulate terrestrial ecosystem responses to atmospheric nitrogen deposition. Ecological Modelling 247, 11-26.

Vesterdal, L., Elberling, B., Christiansen, J.R., Callesen, I., Schmidt, I.K., 2012. Soil respiration and rates of soil carbon turnover differ among six common European tree species. For. Ecol. Manage. 264, 185-196.

Vesterdal, L., Schmidt, I.K., Callesen, I., Nilsson, L.O., Gundersen, P., 2008. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For. Ecol. Manage. 255, 35-48.

Vogt, K., 1991. Carbon budgets of temperate forest ecosystems. Tree Physiology 9, 69-86.

Tables

Table 1. Ground vegetation biomass, depth of humus layer (litter excluded), earthworm abundance and pH in adjacent birch, pine and spruce stands in southern Sweden (n=3 spruce, pine, n=2 birch)

	Silver birch	Scots pine	Norway spruce	Reference
Ground vegetation biomass (g dw m^{-2})	285 n.s.	263	237	(Hansson et al., 2011)
Depth of humus layer	2.1 a	4.7 b	6.7 c	(Hansson et al., 2011)
Earthworm abundance (ind. m^{-2})	119 a	26 b	23 b	(Olsson et al., 2012)
pH(H_2O) humus layer	5.5 a	4.4 b	4.1 c	(Hansson et al., 2011)

Table 2. Stone and boulder percentage to 30 cm depth; clay and sand content at 30 and 70 cm depth and soil geochemistry at 70 cm depth(n=3 spruce, pine, n=2 birch, least squares means±SE). No significant differences between species. Data from Hansson et al. (2011)

		Silver birch	Scots pine	Norway spruce
Stones and boulders	(%)	41.8±7.5	42.5±3.1	39.2±4.8
Clay 30 cm depth	(<0.002mm, %)	3±0	4±0	5±1
Clay 70 cm depth	(<0.002mm, %)	1±0	1±0	2±1
Sand 30 cm depth	(0.02-2mm, %)	87±0	87±2	83±2
Sand 70 cm depth	(0.02-2mm, %)	97±1	96±0	93±2
CaO 70 cm depth	% dw	1.82±0.07	1.72±0.07	1.85±0.09
Fe_2O_3 70 cm depth	% dw	4.21±0.14	4.74±0.48	4.60±0.13
MgO 70 cm depth	% dw	1.04±0.04	0.97±0.09	1.06±0.02
MnO 70 cm depth	% dw	0.077±0.003	0.083±0.008	0.081±0.002

Table 3. References for C and N pools and fluxes used in budget calculations

	Reference
Soil C and N to 30 cm depth (Mg ha^{-1})	(Hansson et al., 2011)
Tree litterfall (Mg ha^{-1} yr^{-1})	(Hansson et al., 2011)
DOC and DON fluxes	(Fröberg et al., 2011a)
Field C and N mineralisation (g m^{-2} yr^{-1})	(Olsson et al., 2012)
Fine root production (g m^{-2} yr^{-1})	(Hansson et al., 2013 this issue)

Table 4. Basal area of dominant tree species (data from Hansson et al. (2011)) and source of functions to estimate tree biomass

Species	Basal area (m^{-2} ha^{-1})	Reference	
	(l s means±SE)	Aboveground biomass	Belowground biomass
Picea abies	29.3±3.8 a	(Marklund, 1988)	(Marklund, 1988)
Pinus sylvestris	20.6±1.1 ab	(Marklund, 1988)	(Marklund, 1988)
Betula pendula	15.4±3.5 b	(Marklund, 1988)	(Repola, 2008)

Table 5. Field and bottom layer longevity estimates and N content used for litter calculations.

	Longevity	% N
Grasses	1.25 year	2.0 (Reich and Oleksyn, 2004)
Forbs	1 year	2.7 (Reich and Oleksyn, 2004)
Ericoids	1.5 year (Karlsson, 1992)	1.4 (Reich and Oleksyn, 2004)
Mosses	5 years (Økland, 1995)	1.6 (T. Persson, pers. comm.)
Trees	Not included, negligible	Not included, negligible

Table 6. Source of functions to estimate understorey aboveground biomass and leaf biomass and N content in litterfall. DBH=diameter at breast height.

Species	Reference biomass			Reference % N
	With DBH	< 130 cm height	Leaf, with/without DBH	Leaf litter
Betula pendula	(Marklund, 1988)	As *F. alnus*	(Johansson, 1999)	(Hansson et al., 2011)
Fagus sylvatica	(Bartelink, 1997)	(Konôpka et al., 2010)	(Bartelink, 1997)/ (Konôpka et al., 2010)	As *B. pendula*
Frangula alnus	y = 3.25E-05x2.9222	y = 3.25E-05x2.9222	Assume 1% of total biomass	As *B. pendula*
Juniperus communis	As *P. abies*, < 130 cm	As *P. abies*	Assume 1% of total biomass	Not included, negligible
Larix spp.	As *P. sylvestris*	As *P. sylvestris*	Assume 1% of total biomass	As *B. pendula*
Malus sylvestris	-	As *B. pendula*	Assume 1% of total biomass	As *B. pendula*
Picea abies	(Marklund, 1988)	(Konôpka et al., 2010)	(Marklund, 1988)/ (Konôpka et al., 2010)	(Hansson et al., 2011)
Pinus sylvestris	(Marklund, 1988)	(Konôpka et al., 2010)	Assume 1% of total biomass	(Hansson et al., 2011)
Quercus robur	As *F. sylvatica*	(Konôpka et al., 2010)	(Konôpka et al., 2010)	As *B. pendula*
Quercus rubra	As *F. sylvatica*	As *Q. robur*	(Konôpka et al., 2010)	As *B. pendula*
Salix spp.	-	As *F. alnus*	Assume 1% of total biomass	As *B. pendula*
Sorbus aucuparia	(Hamburg et al., 1997)	(Hamburg et al., 1997)	Assume 1% of total biomass	As *B. pendula*

Table 7. Adjusted balance in relation to Fig 1 in C fluxes between litter inputs, accumulation of soil organic matter and outputs (g C m^{-2} yr^{-1}) assuming extramatrical mycorrhizal litter (10% of root-litter C, C/N=15) and including an estimate of R_H from fresh litter in the O_i layer.

C	a) Litter-fall	b) Root litter	c) External mycorrh. litter input	d) Σ Litter input (a+b+c)	e) Accum. C	f) R_H (O_i)	g) R_H (Fig. 1)	h) Total R_H (f+g)	i) DOC	Balance (d-e-h-i)
Birch	156	77	7.7	241	-17	62*	160	222	4	32
Pine	208	106	11	325	0	83*	170	253	5	67
Spruce	152	130	13	295	47	61*	270	331	3	-86

* 40% of litterfall

Table 8. Inorganic N available for plant uptake in stands of Norway spruce, Scots pine and silver birch (g N m^{-2} yr^{-1}).

	a) N deposition	b) N leaching	c) Gaseous N losses	d) External balance (a-b-c)	e Net N min.	Estim. plant N uptake (d+e)
Birch	1.0	0.9	?	0.1	8.8	8.9
Pine	1.0	0.7	?	0.3	8.2	8.5
Spruce	1.5	0.2	?	1.3	8.2	9.5

Table 9. Internal (N deposition and N leaching excluded) balance in relation to Fig 2 in N fluxes between litter inputs, accumulation of soil organic matter and outputs (g N m^{-2} yr^{-1}) assuming extramatrical mycorrhizal litter (10% of root-litter N, C/N=15). The O_i layer was assumed to have no net N mineralisation.

N	a) Litter-fall	b) Root litter	c) External mycorrh. litter input	d) Σ Litter input (a+b+c)	e) Accum. N	f) N min (O_i)	g) N min (Fig. 2)	h) Total net N min (f+g)	Balance (d-e-h)
Birch	5.6	2.1	0.5	8.2	-0.4	0	8.8	8.8	-0.2
Pine	5.6	2.7	0.7	9.0	0	0	8.2	8.2	0.8
Spruce	4.4	3.3	0.9	8.6	1.6	0	8.2	8.2	-1.2

Table 10. Mean residence time (MRT, years ±SE) estimated as the quotient between the C pool (g C m^{-2}) and heterotrophic respiration [R_H, g CO_2-C (g C)$^{-1}$ yr^{-1}] in each soil layer in the tree-species experiment at Tönnersjöheden.

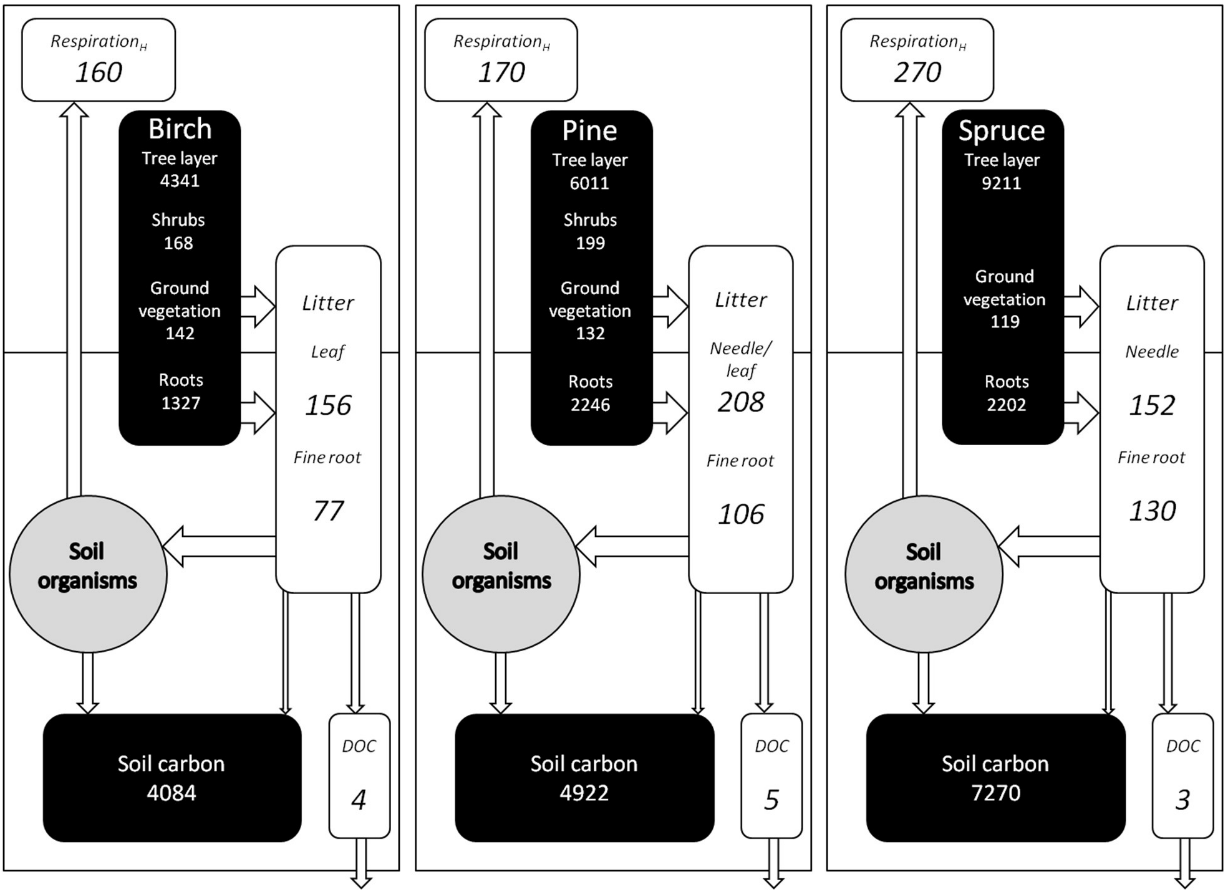
Means±SE	Oe+Oa	0-10 cm	10-20 cm	20-30 cm
Birch	9.5±0.8	47±9.1	101±15	140±29
Pine	23±8.9	49±17	105±45	157±50
Spruce	31±1.9	62±9.9	120±27	205±12

Figure captions

Fig. 1. Estimated C pools (g C m^{-2}) and fluxes (g C m^{-2} yr^{-1}) in 50-year-old birch, pine and spruce stands. Pools are displayed in black boxes, fluxes in white. Litter inputs (woody debris, coarse roots and fungal litter excluded) and heterotrophic respiration (R_H; Oi layer excluded) are underestimated.

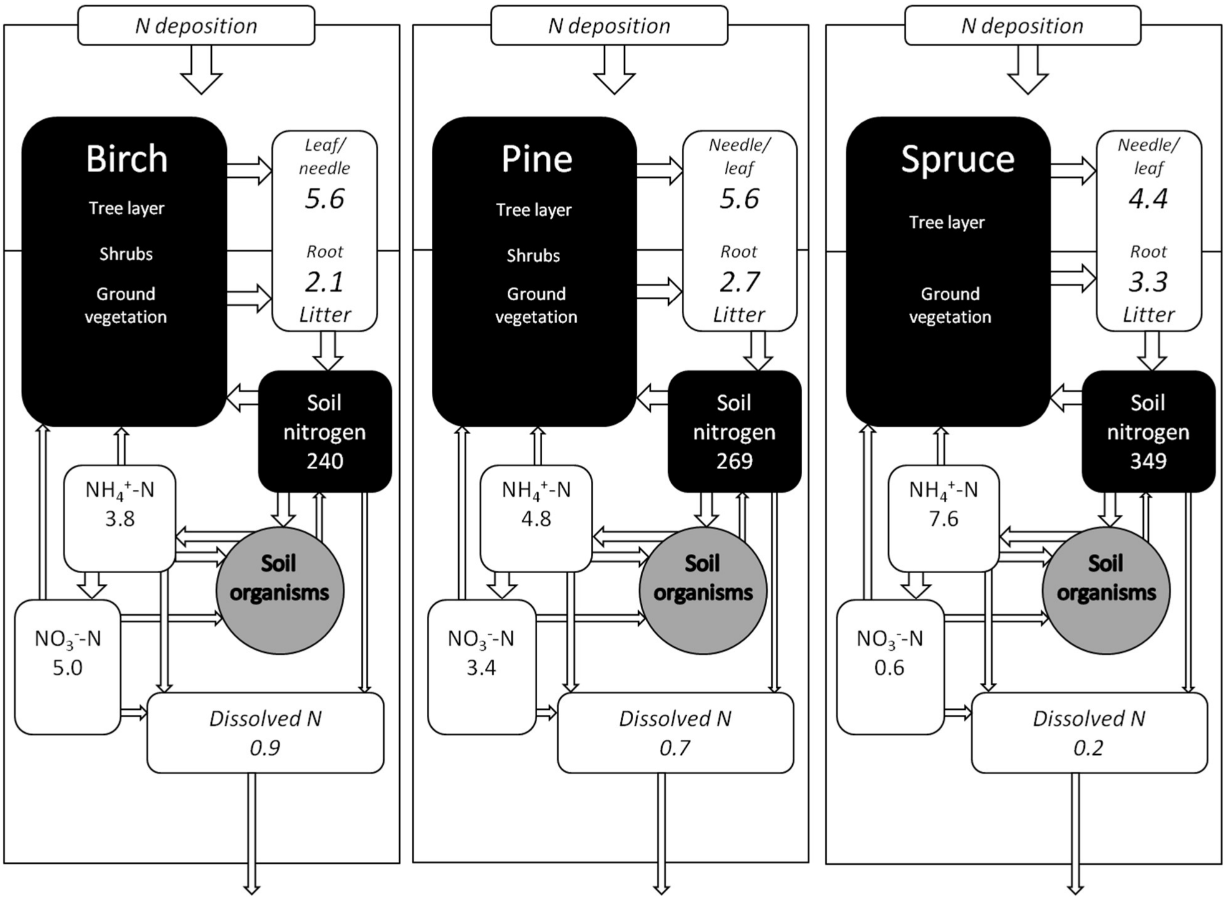
Fig. 2. Estimated N pools (g N m^{-2}) and fluxes (g N m^{-2} yr^{-1}) in birch, pine and spruce stands. Pools are displayed in black boxes, fluxes in white. The figures given for NH_4^+ and NO_3^- denote rates viewed over a period of 30 days. Litter inputs (woody debris, coarse roots and fungal litter excluded) are underestimated.

Figure 1.



Respiration_H
160
Birch
Tree layer
4341
Shrubs
168
Ground vegetation
142
Roots
1327
Litter
Leaf
156
Fine root
77
Soil organisms
Soil carbon
4084
DOC
4
Respiration_H
170
Pine
Tree layer
6011
Shrubs
199
Ground vegetation
132
Roots
2246
Litter
Needle/ leaf
208
Fine root
106
Soil organisms
Soil carbon
4922
DOC
5
Respiration_H
270
Spruce
Tree layer
9211
Ground vegetation
119
Roots
2202
Litter
Needle
152
Fine root
130
Soil organisms
Soil carbon
7270
DOC
3

Fig 2.



N deposition
Birch
Tree layer
Shrubs
Ground vegetation
Leaf/ needle
5.6
Root
2.1
Litter
Soil nitrogen
240
NH_4^+-N
3.8
NO_3^--N
5.0
Soil organisms
Dissolved N
0.9
N deposition
Pine
Tree layer
Shrubs
Ground vegetation
Needle/ leaf
5.6
Root
2.7
Litter
Soil nitrogen
269
NH_4^+-N
4.8
NO_3^--N
3.4
Soil organisms
Dissolved N
0.7
N deposition
Spruce
Tree layer
Ground vegetation
Needle/ leaf
4.4
Root
3.3
Litter
Soil nitrogen
349
NH_4^+-N
7.6
NO_3^--N
0.6
Soil organisms
Dissolved N
0.2