Impact of Tree Species on Carbon in Forest Soils

Karna Hansson
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala

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Cover: Birch, pine and spruce stands at Tönnersjöheden
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Abstract

Different tree species differ in productivity, litter quality and quantity, canopy structure and nitrogen deposition. Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *B. pubescens*) are the three dominant tree species in Sweden. This thesis compares soil C fluxes and the accumulation of soil organic carbon under adjacent Norway spruce, Scots pine and silver birch stands growing on similar soils and examines the different processes involved. This was achieved mainly through field measurements of carbon pools and fluxes in southern Sweden, combined with respiration and decomposition studies in the laboratory.

Soil carbon fluxes and the accumulation of soil organic carbon were found to differ between the three species, with the strongest differences in humus layers between spruce and birch, with pine intermediate. Most carbon was stored in soils in spruce stands. Birch stands had the fastest root turnover and the highest carbon mineralisation rate.

Species differences can be explained by differences in tree growth rate and decomposition. The three tree species differed in terms of litter quality, carbon mineralisation, DOC fluxes and fine root turnover.

Keywords: Pinus silvestris, Picea abies, Betula pendula, fine root, carbon, nitrogen, soil, DOC

Author's address: Karna Hansson, SLU, Department of Ecology,
P.O. Box 7044 Uppsala, Sweden
E-mail: karna.hansson@slu.se

Blott en dag, ett ögonblick i sänder

Lina Sandell

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hansson K., Kleja D.B., Kalbitz K., Larsson H. (2010). Amounts of carbon mineralised and leached as DOC during decomposition of Norway spruce needles and fine roots. *Soil Biology & Biochemistry* 42, 178-185.

II Hansson K., Olsson B., 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. *Forest Ecology and Management* 262, 522-530.

III Fröberg M., Hansson K., Kleja D.B., Alavi G. (2011). Dissolved organic carbon and nitrogen leaching from Norway spruce, Scots pine and silver birch stands in southern Sweden. *Forest Ecology and Management,* in press. DOI: 10.1016/j.foreco.2011.07.033

IV Olsson B.A., Hansson K., Persson T., Beuker E., Helmisaari, H-S. Heterotrophic respiration and nitrogen mineralisation in soils of Norway spruce, Scots pine and silver birch stands in contrasting climates (manuscript).

V Hansson K., Helmisaari H-S., Sah S., Lange H. Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden (manuscript).

The contribution of Karna Hansson to the papers included in this thesis was as follows:

I Main author. Main responsibility for laboratory work. Idea development, maintenance of the experiment, interpretation of data together with co-authors.

II Main author. Main responsibility for field work. Idea development and interpretation of data together with co-authors.

III Co-author. Idea development, interpretation of data together with co-authors.

IV Co-author. Main responsibility for laboratory work. Idea development, interpretation of data together with co-authors.

V Main author. Main responsibility for field work, laboratory work and image analyses. Idea development, interpretation of data together with Heljä-Sisko Helmisaari.

Abbreviations

DBH	Diameter at breast height
DN	Dissolved nitrogen
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
KM	Kaplan-Meier
SOM	Soil organic matter
SRL	Specific root length
SUVA	Specific ultraviolet absorbance

1 Introduction

1.1 Carbon dynamics in forests

Net emissions of the greenhouse gas carbon dioxide (CO_2) to the atmosphere are affected by carbon sinks and sources. Estimates show that European forest ecosystems are an important carbon sink (e.g. Luyssaert *et al.*, 2010). Many different factors, such as tree growth, understorey vegetation, dissolved organic matter (DOM) leaching and organic matter decomposition rate, affect the carbon pools and fluxes in forest ecosystems (Fig. 1).

The main part of the sink is sequestration of carbon (C) in biomass but a substantial part is stored in the soil as soil organic matter (SOM). Main C inflows to the soil are from aboveground (mainly leaf litter) and belowground (root) litter. In addition to that removed with harvest, C is lost through respiration and through dissolved organic carbon (DOC) leaching with soil water (Fig 1).

The carbon sink is closely linked to nitrogen (N) cycling, mainly through tree growth and litter decomposition (Fig. 1). The main N inflows are deposition and fixation, while harvest and leaching are the most important N outflows (e.g. Akselsson *et al.*, 2007).

1.2 Tree species differences

Different tree species differ in productivity, litter quality and quantity, canopy structure and nitrogen deposition. Forest management alters species composition and affects the size of the carbon sink.

As a result of climate change, with changes in humidity and temperature, tree species composition in unmanaged forests in Sweden is predicted to change, with deciduous species spreading towards the north (Koca *et al.*, 2006). In addition, tree species composition in managed forests may change.

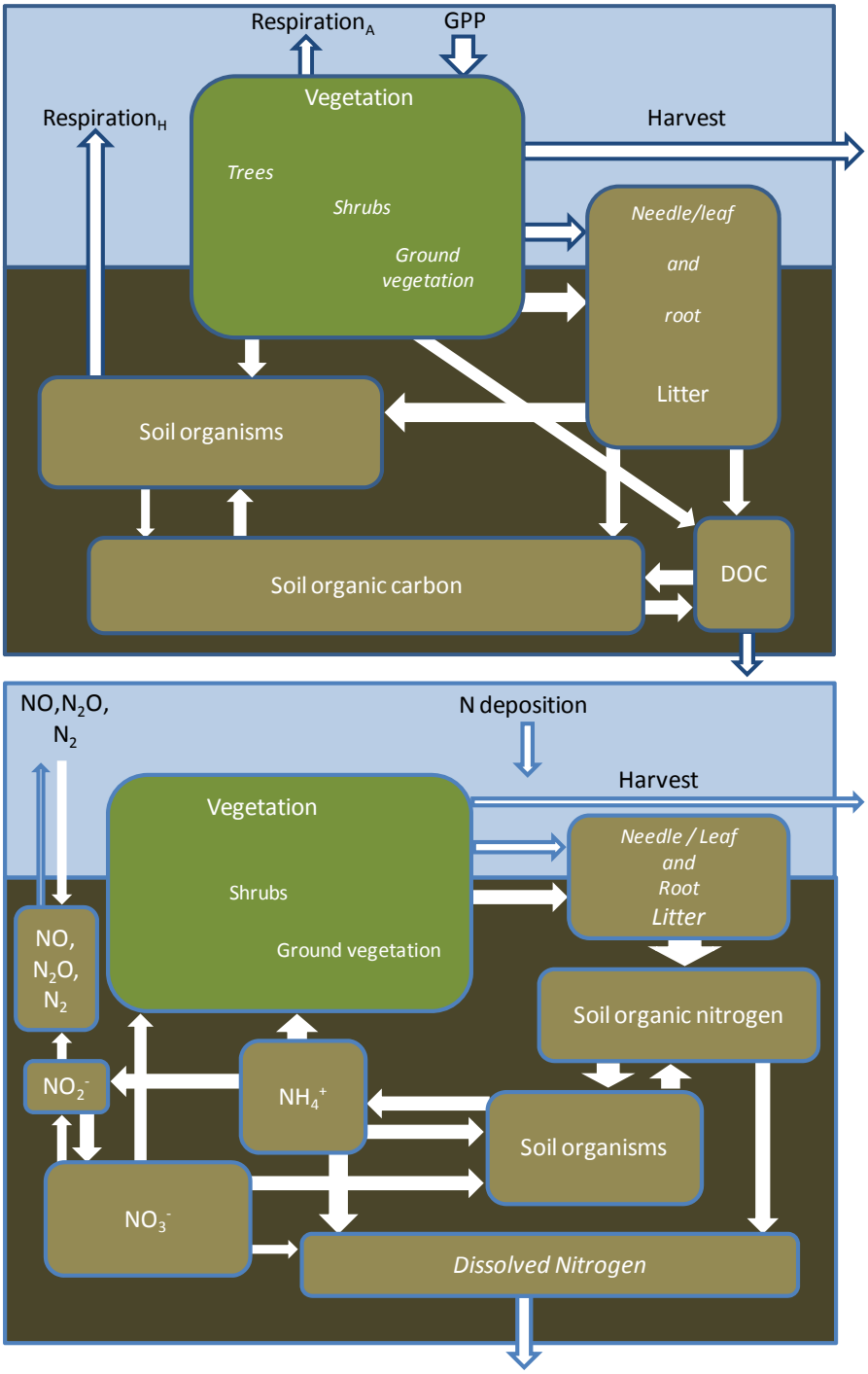

Figure 1. Simplified carbon (C) cycle (upper diagram) and nitrogen (N) cycle (lower diagram) in forests.

This in turn has the potential to change production, turnover and sequestration of carbon in vegetation and soil.

Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *B. pubescens*) are the three dominant tree species in Sweden, comprising 41, 39 and 13% of standing volume of forests respectively (Anonymous, 2010). They are thus of major importance for carbon sequestration in Swedish forests. In southern Sweden the relative proportions are 45% spruce, 30% pine and 11% birch and this region tends to have a higher percentage of deciduous species, 25% compared with 17-19% in northern Sweden. Although spruce is now the most common species even in the southernmost parts of Sweden, this has not always been the case. Spruce was introduced about 150 years ago in this part of the country (Malmström, 1937; Hesselman & Schotte, 1906), whereas pine and birch have been present for a long time.

Birch, pine and spruce affect soil properties in different ways. Birch has a lower growth rate than spruce in southern Sweden, with pine intermediate (Anonymous, 2010; Ekö *et al.*, 2008). Litter input and quality differs between the species; birch is a deciduous tree, shedding its leaves every autumn, whereas pine and spruce are coniferous. Pine needle longevity is about 2-4 years, whereas spruce needle longevity is often more than 6 years (Reich *et al.*, 1996).

Although it is well known that soil properties differ between stands of different species, few studies have been able to separate the effect of species on soil properties from the confounding effects of soil properties on type of stand. Specifically, there is a lack of studies that experimentally compare the influence of the three dominant tree species in southern Sweden on soil carbon.

2 Aims

The overall aim of this thesis was to compare soil C fluxes and the accumulation of soil organic carbon under Norway spruce, Scots pine and silver birch stands growing on similar soils and to obtain information on the different processes involved. This was achieved mainly through field measurements of carbon pools and fluxes in southern Sweden, combined with respiration and decomposition studies in the laboratory.

Specific aims of the different papers were to:

1. Qualitatively and quantitatively compare dissolved organic matter (DOM) leached from spruce root and needle litter at different stages of decomposition (Paper I).
2. Compare differences in soil properties, such as soil texture, carbon, nitrogen and base cation content and pH, in adjacent pine, spruce and birch stands in southern Sweden (Paper II).
3. Compare differences in dissolved organic carbon and nitrogen leaching from adjacent pine, spruce and birch stands in southern Sweden (Paper III).
4. Compare differences in carbon and nitrogen mineralisation in soils from pine, spruce and birch stands in southern Sweden and northern Finland (Paper IV).
5. Quantify fine root biomass, production and turnover in pine, spruce and birch stands in southern Sweden (Paper V).

3 Study sites

Data were obtained from three different study sites, two in southern Sweden and one in northern Finland (Fig. 2).

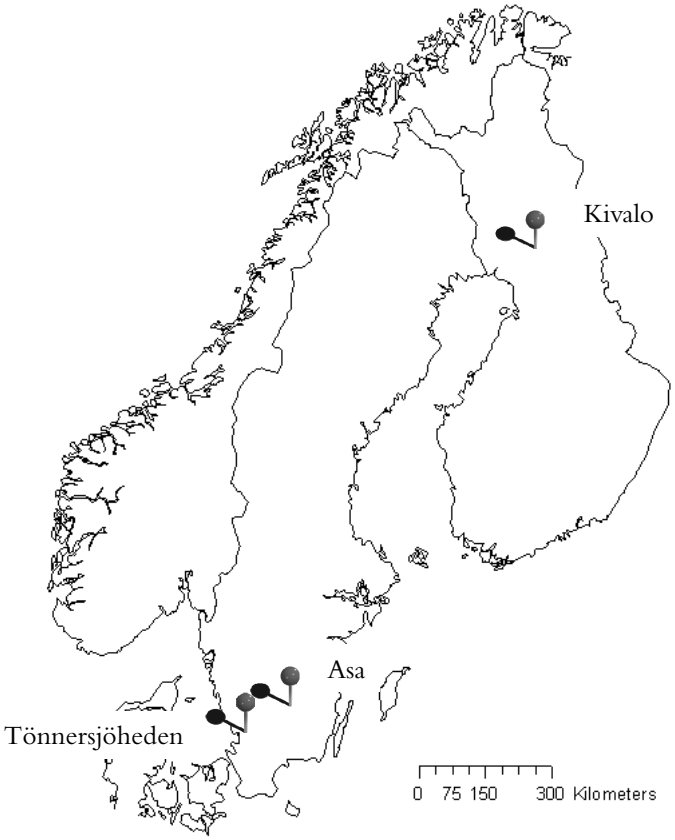

Figure 2. Location of the study sites, from south to north: Tönnersjöheden, Asa, Kivalo.

3.1 Tönnersjöheden (Papers II-V)

Tönnersjöheden Experimental Forest is located in south-west Sweden (56°40-41'N, 13°03-06'E), at 70-90 m above sea level. Tönnersjöheden is in the temperate vegetation zone, but close to the hemiboreal zone. Mean annual air temperature is 6.4 °C and mean annual precipitation is 1053 mm. Length of the growing season is 204 days. The soil parent material is of glacifluvial origin.

The experiment 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). Most plots used were established earlier as part of other experiments. A survey of the Tönnersjöheden Experimental Forest by Malmström (1937) indicated that in 1890, blocks 1 and 2 in the present study area were heather moorland with some 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 dominated by 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 and the basal area of the established overstorey trees, measured in 2009/2010, varies from 12.3 to 37.5 $m^2 ha^{-1}$. Spruce stands have the highest average basal area, 29.3 $m^2 ha^{-1}$, followed by 20.6 $m^2 ha^{-1}$ for pine and 15.4 $m^2 ha^{-1}$ for birch stands.

3.2 Asa (Paper I)

In the decomposition study (Paper I), Norway spruce needle and root material was taken from Asa Experimental Forest (57°08'N, 14°45'E). Asa is located 190-200 m above sea level in the hemiboreal zone in southern Sweden. The soil, a Haplic Podzol, is developed on a glacial till.

This study used existing sites established within the LUSTRA research programme (Kleja *et al.*, 2008; Berggren *et al.*, 2004). Stand age was 44-47 years in 2007. Mean annual air temperature at the site is 5.5 °C and mean annual precipitation is 688 mm. Site productivity ranges from 10.1 to 11.3 $m^3 ha^{-1} yr^{-1}$. Field and ground vegetation is grass or no vegetation.

3.3 Kivalo (Paper IV)

Kivalo is located in northern Finland (66°20'N/26°40'E), at 250 m above sea level, in the northern boreal zone, near the Arctic Circle. The soils are glacial till on Precambrian rock and the soil type is podzolic.

The site was previously a homogeneous spruce stand, clearcut in 1926, after which stands of Norway spruce, Scots pine and silver birch were established. Average basal area of the dominant tree species was 21.3, 20.0 and 20.8 m^2 ha^{-1} for birch, spruce and pine respectively in 2002 (Smolander & Kitunen, 2002). Ground vegetation cover varies between the stands, with more herbs and grasses in the birch stand than in the coniferous stands. Soil samples from three existing study plots (Smolander & Kitunen, 2002) in each stand were used to study differences in heterotrophic respiration between Kivalo and Tönnersjöheden (Paper IV).

4 Methods

A general description of the methods used is provided below. For further details, see Papers I-V.

4.1 Soil

4.1.1 Soil texture and geochemistry (Paper II)

In order to verify that all plots at Tönnersjöheden had similar parent material, soil samples were taken from 30 and 70 cm depth for texture analyses, and from 70 cm depth for geochemical analyses of the parent material. The stoniness, to a depth of 30 cm, was measured in each stand and calculated according to Stendahl *et al.* (2009) modified from Viro (1952).

4.1.2 Soil chemistry (Paper II)

Soil samples for chemical analyses were taken from the humus layer (litter layer not included) and from 0-10 cm, 10-20 cm and 20-30 cm depth in the mineral soil at Tönnersjöheden. Total amounts of C, N and exchangeable cations were determined, as was pH. Effective cation exchange capacity (CEC_{eff}) was determined as the sum of the extractable amounts of H^+, Na^+, K^+, Ca^{2+}, Mg^{2+} and Al^{3+} at soil pH. Base saturation was calculated as the equivalent sum of base cations (Ca, Mg, K, and Na) divided by CEC_{eff}.

4.1.3 Soil water (Paper III)

In each plot at Tönnersjöheden, three zero-tension lysimeters, (30 cm squares, made of plexiglass and a polyethylene net) were installed under the O-horizon. Under the A-horizon, at 10-16 cm depth from the soil surface, two Prenart Soil Disc lysimeters per plot were installed. Under the B-horizon, at 42-50 cm depth from the soil surface, two Prenart Super Quartz

lysimeters were installed. Water was collected monthly and pooled per plot and horizon prior to DOC and dissolved nitrogen analysis. Analyses of total organic C and total N were made, UV absorbance was measured at 260 nm and pH was measured on all pooled samples. Specific ultraviolet absorbance at 260 nm ($SUVA_{260}$) was calculated as absorbance divided by DOC concentration.

Water fluxes were simulated using Coup Model (Jansson & Karlberg, 2004). The driving climate variables were daily sum of precipitation, daily averages of air temperature, air humidity, wind speed and solar radiation. Soil hydraulic parameters were estimated for each plot using the measured soil texture and pedofunctions. Leaf area index (including that of the understorey) was measured in each plot during summer 2010. Root density was estimated from measured root biomass.

4.1.4 Heterotrophic soil respiration (Paper IV)

Soil samples were collected from the humus layer and from 0-10 and 10-20 cm depth in the mineral soil at Tönnersjöheden and Kivalo. Samples were sieved and the fresh material from each sample was carefully mixed and divided into a number of sub-samples to be used to determine dry matter content, soil pH, total C and N concentrations, inorganic N concentration, and water-holding capacity. Another sub-sample was used for C and N mineralisation studies.

After sample preparation, humus and mineral soil were placed in plastic jars, each with a lid with a 5-mm diameter aperture for gas exchange. These soil microcosms were incubated for 30 days at a constant temperature of 15 °C. CO_2 measurements were performed once a week after the starting day, and the mean CO_2 evolution rate per day was based on the cumulative estimates up to day 30.

To determine C mineralisation in the litter and soil materials, the containers were periodically closed with airtight lids with a rubber septum. Background gas samples were taken with a syringe from the headspace after 15 minutes and injected into a gas chromatograph. The measurements were repeated when an appropriate amount of CO_2 had accumulated in the containers, after 2 h (litter and humus) to about 5 h (mineral soil), depending on the respiration rate.

Carbon mineralisation rate was generally expressed as g CO_2-C g^{-1} C day^{-1}, and quantitative data on the C pools in each soil layer allowed C mineralisation rate 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, estimated C mineralisation was assumed to be of heterotrophic and not autotrophic origin. Potential

net N mineralisation and nitrification were calculated and rates were expressed as μg N $(g\ C)^{-1}\ d^{-1}$.

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, (3) a temperature-dependent factor and (4) a moisture-dependent factor.

4.1.5 Earthworm abundance (Paper IV)

To determine the abundance of earthworms (Oligochaeta), the soil at Tönnersjöheden was sampled in September 2010. Samples were taken down to 15 cm depth from the litter surface. Earthworms were extracted using Tullgren funnels (3 days), counted and species-determined under a binocular microscope.

4.1.6 Mycelia production (Paper V)

Fungal in-growth bags (mesh size 50 μm) filled with acid-washed sea sand (5 per plot at Tönnersjöheden) were left in the forest soil, about 5 cm from the soil surface, in October 2006 and collected two years later. Amount of mycelia in the mesh bags was estimated on a scale of 0-5, using visual criteria, with 0 having no visual mycelia and 5 having almost the entire mesh bag full of fungal aggregates. The sand was then carefully mixed and samples were taken for analysis of ergosterol content, carried out according to Wallander (2011).

4.2 Vegetation

4.2.1 Tree biomass and litterfall (Paper II)

Tree basal area and height of the different stands at Tönnersjöheden were measured in 2009-2010 and aboveground and belowground biomass calculated using correlation functions from the literature (Table 1). Carbon content was estimated as 50% of biomass.

Table 1. *Basal area of dominant tree species and source of functions to estimate tree biomass*

Species	Basal area ($m^{-2}\ ha^{-1}$)	Reference	
		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)

Litterfall in Tönnersjöheden plots was collected during three years, from April 2007 to April 2010, with nine litter traps (2 m height) in each plot. Litter was sorted into two fractions, with cones and twigs with a diameter larger than 1 cm separated from the rest of the material. Both fractions were weighed and the finer fraction was further analysed. Total amounts of C, N, Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S and Zn were determined.

4.2.2 Understorey vegetation (Paper II)

Understorey vegetation was defined as bottom and field layer 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. At Tönnersjöheden it was divided into two groups; bottom and field layer, defined as vegetation <50 cm height, and shrub layer, >50 cm height. The bottom and field layer was further subdivided into grasses, forbs, ericoids, mosses and tree seedlings.

To determine field and bottom layer vegetation aboveground biomass, eight sampling squares were selected along a transect in each plot. In each square ($40\times40 cm^2$ for birch and pine, $15\times15 cm^2$ for spruce), all vegetation shorter than 50 cm was harvested, sorted (grasses, forbs, ericoid dwarf shrubs, mosses, trees), weighed and dried.

Litter input from field and bottom layer was calculated as biomass divided by estimated longevity (Table 2). For ericoid dwarf shrubs, leaf biomass was assumed to be 25% of total biomass.

Table 2. *Field and bottom layer biomass at Tönnersjöheden and longevity estimates used for litter calculations*

	Biomass (g dw m^{-2}):			Reference,
	Birch plots	Pine plots	Spruce plots	longevity
Grasses	157±11 a	119±35 a	0±0 b	1.25 year
Forbs	25±6	22±8	0±0	1 year
Ericoids	17±15	69±27	0±0	1.5 year (Karlsson, 1992)
Mosses	69±12 ab	38±3 a	237±61 b	5 years (Økland, 1995)
Trees	10±5	15±11	0±0	Not included, negligible

The spruce plots did not have any 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 were measured (at root collar and, when applicable, at breast height, 130 cm) of each tree/shrub. Aboveground biomass was estimated using correlations between diameter, height, volume and biomass. For most

species these correlation functions were taken from the literature (Table 3), but for *Frangula alnus,* 10 shrubs of different sizes were harvested and the correlation function calculated. For some species the correlation was assumed to be the same as for other, similar species.

Table 3. *Source of functions to estimate understorey aboveground biomass and leaf biomass. DBH=diameter at breast height.*

Species	Reference		
	With DBH	< 130 cm height	Leaf, With/without DBH
Betula pendula	(Marklund, 1988)	As *F. alnus*	(Johansson, 1999)
Fagus sylvatica	(Bartelink, 1997)	(Konôpka *et al.*, 2010)	(Bartelink, 1997), (Konôpka *et al.*, 2010)
Frangula alnus	y = 3.25E-05x2.9222	y = 3.25E-05x2.9222	Assume 1% of total biomass
Juniperus communis	As *P. abies*, < 130 cm	As *P. abies*	Assume 1% of total biomass
Larix spp.	As *P. sylvestris*	As *P. sylvestris*	Assume 1% of total biomass
Malus sylvestris	-	As *B. pendula*	Assume 1% of total biomass
Picea abies	(Marklund, 1988)	(Konôpka *et al.*, 2010)	(Marklund, 1988), (Konôpka *et al.*, 2010)
Pinus sylvestris	(Marklund, 1988)	(Konôpka *et al.*, 2010)	Assume 1% of total biomass
Quercus robur	As *F. sylvatica*	(Konôpka *et al.*, 2010)	(Konôpka *et al.*, 2010)
Quercus rubra	As *Q. robur*	As *Q. robur*	(Konôpka *et al.*, 2010)
Salix spp.	-	As *F. alnus*	Assume 1% of total biomass
Sorbus aucuparia	(Hamburg *et al.*, 1997)	(Hamburg *et al.*, 1997)	Assume 1% of total biomass

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 3), but for some species leaf biomass was simply assumed to be 1% of total biomass. Leaf longevity was estimated to be 6 for spruce and 1 for other species. Carbon content was estimated as 50% of biomass.

4.2.3 Fine root biomass (Paper V)

Soil samples were taken from the humus layer (litter layer not included) and from 0-10 cm, 10-20 cm and 20-30 cm depth in the mineral soil at Tönnersjöheden. Roots were cleaned and sorted into tree and ground vegetation roots. Living tree roots were sorted into fine roots (<2 mm) and coarse roots (>2 mm). The fine root fraction was further sorted into roots with <0.5 mm, 0.5-1 mm and 1-2 mm diameter. Roots were dried before determination of biomass.

Figure 3. Minirhizotron tube with root camera. Photo: K. Hansson.

4.2.4 Fine root production and turnover (Paper V)

The lifetime distribution of roots from birch, pine, spruce and ground vegetation was estimated based on observations made using the minirhizotron method. The measurement period comprised four seasons (2007-2010) and contained 14 different sessions. Acrylic minirhizotron tubes were installed in all plots at Tönnersjöheden, three vertically and two horizontally in the humus layer. Image acquisition started one year after installation, to allow stabilisation of the soil around the tubes. Roots were photographed during the growing season, two to six times per year, for four years, 2007-2010 (Fig. 3). For each tube, images from the humus layer and the upper 10 cm in the mineral soil were analysed together. Deeper soil layers were excluded, since very few roots were seen in the mineral soil. Roots were traced and for each root segment, diameter and length were measured. Roots were sorted into birch, pine, spruce (Fig. 4) and understorey vegetation, the last group including mainly grasses and forbs, but also some undefined understorey tree roots. For each session, roots were classified as alive or gone. Live and dead roots are often separated using differences in colour, with white roots defined as live and those turning black defined as dead (e.g. Majdi & Andersson, 2005). This distinction was not possible in our case, partly due to image quality, but mainly due to large colour variations in live roots depending on mycorrhizal type, with many examples of roots appearing black, but still growing (see also e.g. Gaul *et al.*, 2009; Withington *et al.*, 2006). The number of roots in the set (considering

every root section as a individual unit) was high. However, the sessions were not evenly distributed over the seasons due to camera problems.

To estimate the lifetime distribution of the roots, two different methods were used; the Kaplan-Meier product limit method (Kaplan & Meier, 1958), or KM for short, and fitting a Weibull distribution (Weibull, 1951) to the observations.

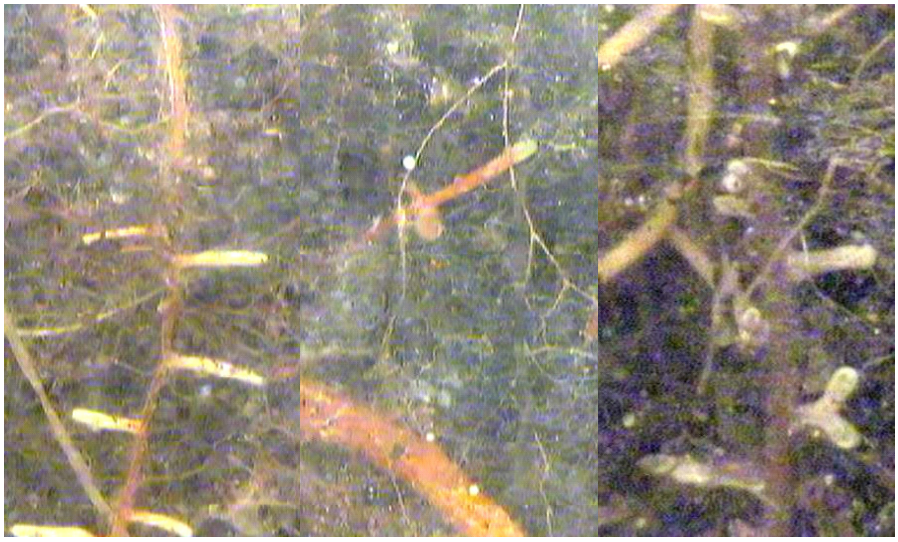

Figure 4. Minirhizotron images with birch (left), spruce (centre) and pine (right) mycorrhizal root tips.

The two approaches are not subtle variations but fundamentally different in their assumptions and mathematics. Nevertheless, for infinitely many subjects (roots in the present case) and infinitely many observations, they lead to the same asymptotic distribution. Thus, should the estimators (median or mean longevity, variance) be similar, it can be concluded that they are reliable and sample size is probably sufficient.

The KM approach is a nonparametric method based on the empirical cumulative distribution function. The Weibull distribution follows a parametric approach, fitting 'time-to-failure' data to a prescribed distribution.

Common to both approaches was a stratification of the results according to tree species plus ground vegetation, and root diameter in discrete classes.

4.2.5 Decomposition of needles and fine roots (Paper I)

Five different litter types were sampled at Asa: fresh needle litter, aged needles from litter layer, fresh roots from mineral soil, dead roots from

mineral soil and seven-year-old roots from a previous litterbag study. Litter samples were incubated in glass columns, using a method adapted from Sjöberg *et al.* (2003). Prior to the start of the experiment, litter samples were inoculated with a litter extract from the site (Asa).

Production of CO_2 was measured after 1, 2, 3, 6, 9, 12, 15, 19 and 28 weeks of incubation. Glass columns were closed with an airtight lid, and CO_2 was measured using a gas chromatograph, as described for heterotrophic respiration. On the day after CO_2 measurements, the columns were percolated with 50 mL throughfall water solution. Leachate was analysed for DOC concentration, pH and UV absorbance at 285 nm. Specific ultraviolet absorbance at 285nm ($SUVA_{285}$) was calculated as absorbance divided by DOC concentration.

To determine carbon mineralisation of leachate obtained after 12 weeks of the column experiment, samples were incubated in sealed flasks for 8 weeks. Nutrients were added in order to adjust the C:N ratio and facilitate DOM biodegradation. For inoculation, a uniform microbial community was chosen for all samples so that any variation measured would only be the result of variation in DOM properties. CO_2 was measured 7 times during the incubation period, at short intervals at the beginning of the experiment and at long intervals at the end.

Sorption of dissolved organic matter (DOM) in mineral soil horizons is probably the main process by which DOM is retained in forest soils (Kalbitz *et al.*, 2005). In Sweden, 60% of all forest soils are podzolic, with most soil organic matter concentrated in the iron-rich B-horizon (Olsson *et al.*, 2009). The ability of DOM to be sorbed by ferrihydrite was investigated on leachate obtained after 6, 9 and 19 weeks.

5 Impact of tree species on soil carbon

Soil C fluxes and the accumulation of soil organic carbon at Tönnersjöheden differed between the three species, with the strongest differences between spruce and birch, with pine intermediate (Fig. 5). Even though there are still a few pieces missing in this puzzle, it is clear that tree species is an important factor to take into account when estimating carbon pools and fluxes.

At Tönnersjöheden, 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 same basal area.

Table 4. *Stone and boulder percentage to 30 cm depth; sand and clay content at 30 and 70 cm depth and soil geochemistry at 70 cm depth at Tönnersjöheden (n=3 spruce, pine, n=2 birch, least squares means±SE). No significant differences between species*

		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

It is well known that soil properties differ between stands of different species, but few studies have been able to separate the effect of species on soil properties from the confounding effects of soil properties on type of stand. One aim of this study was to compare pine, spruce and birch stands on similar soils. The analyses revealed no significant differences in soil type, texture or geochemistry (Table 4; Paper II), and therefore confirmed that the experimental plots at Tönnersjöheden have similar backgrounds, justifying the attribution of observed stand differences to tree species.

5.1 Carbon pools (Papers II, V)

Estimated carbon pools were soil C, down to 30 cm depth in mineral soil and C in aboveground and belowground plant biomass. The strongest species differences were displayed in the humus layer, partly explained by differences in humus layer thickness (spruce stands 6.7 cm, pine stands 4.7 cm, birch stands 2.1 cm), but also differences in organic matter quality.

5.1.1 Soil carbon and nitrogen (Paper II)

The total soil carbon pool (humus layer and 0-30 cm mineral soil) was significantly larger in spruce stands (7270 g m^{-2}) than in pine (4922 g m^{-2}) and birch stands (4084 g m^{-2}). Soil nitrogen followed the same distribution pattern as soil carbon. Total amount of N was significantly larger in spruce stands (349 g m^{-2}) than in birch stands (240 g m^{-2}), with pine (269 g m^{-2}) intermediate. In the humus layer, the amount of C and N differed significantly between species, spruce>pine>birch (Fig. 5).

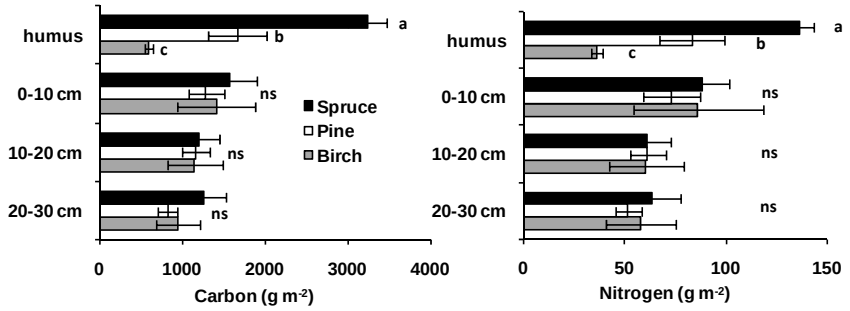

Figure 5. Differences in amount of carbon (g m^{-2}) and nitrogen (g m^{-2}) at different soil depths (n=3 spruce, pine, n=2 birch; least squares means±SE). Different letters indicate significant differences between species ($P<0.05$), ns = not significant.

Weighted average C:N ratio for the entire profile, i.e. the ratio between total amount of C and N in the profile, was significantly lower for birch

(17) and pine stands (18) than for spruce stands (20), with a similar pattern for the humus layer.

5.1.2 Tree and understorey biomass (Papers II, V)

Tree basal area was significantly larger in spruce stands than in birch stands at Tönnersjöheden, with spruce intermediate (Table 1), indicating higher production in spruce stands. The estimated carbon pool in total aboveground and belowground biomass, including understorey vegetation, was also largest in spruce stands (11531 g C m^{-2}), followed by pine (8588 g C m^{-2}) and birch (5979 g C m^{-2}) stands.

Total tree fine root biomass was significantly higher in spruce stands (702 g m^{-2}) compared with birch (196 g m^{-2}) and pine (227 g m^{-2}) stands. Fine root distribution followed the same pattern for pine and spruce, with most biomass in the organic layer and decreasing with depth, whereas birch had few roots in the thin organic layer and increased root biomass in the upper part of the mineral soil (Fig. 6).

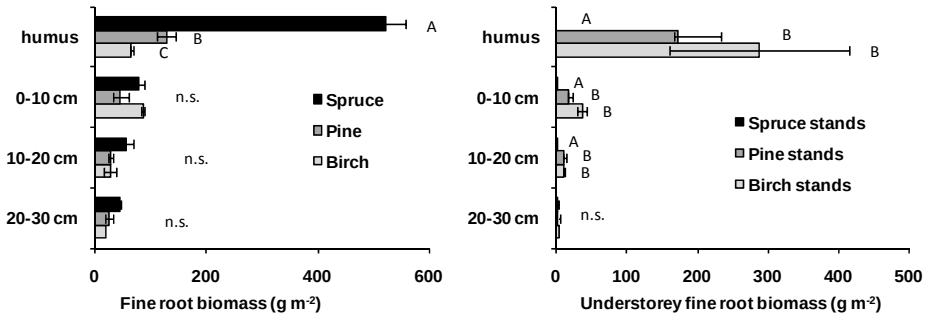

Figure 6. Differences in fine root (diameter <2 mm) biomass at different soil depths for (left) spruce, pine and birch (n=3 spruce, pine stands, n=2 birch stands; least squares means±SE) and (right) understorey vegetation (n=3 spruce, pine stands, n=2 birch stands; means±SE). Different letters indicate significant differences between species (P<0.05).

In spruce stands at Tönnersjöheden, the only understorey vegetation was a bottom layer of mosses, whereas pine and birch stands had a field layer with a mixture of grass, forbs, ericoid dwarf shrubs, mosses and small trees, as well as a shrub layer with many different species, including suppressed trees (*cf.* Tables 2 & 3).

Total understorey fine root biomass did not differ significantly between pine (205 g m^{-2}) and birch (337 g m^{-2}) stands, but was significantly lower in spruce stands (4 g m^{-2}) (Fig. 6).

5.2 Soil carbon inflows (Papers II, V)

Estimated carbon inflows to soil consisted of aboveground litterfall, both from trees and understorey, and fine root turnover.

5.2.1 Litterfall (Paper II)

Annual litterfall was significantly higher in pine (137 g C m^{-2} yr^{-1}) and spruce (128 g C m^{-2} yr^{-1}) stands compared with birch stands (72 g C m^{-2} yr^{-1}). Litterfall from understorey trees and shrubs higher than 2 m was included in the measured litterfall. Estimated litterfall from shrubs and ground vegetation was highest in birch stands (84 g C m^{-2} yr^{-1}), compared with those of pine (71 g C m^{-2} yr^{-1}) and spruce (24 g C m^{-2} yr^{-1}). Understorey vegetation may be one reason why soil properties in pine stands in many ways resembled birch more than spruce soils did. Most of the understorey vegetation was deciduous, with litter quality probably more like birch litter than pine and spruce litter.

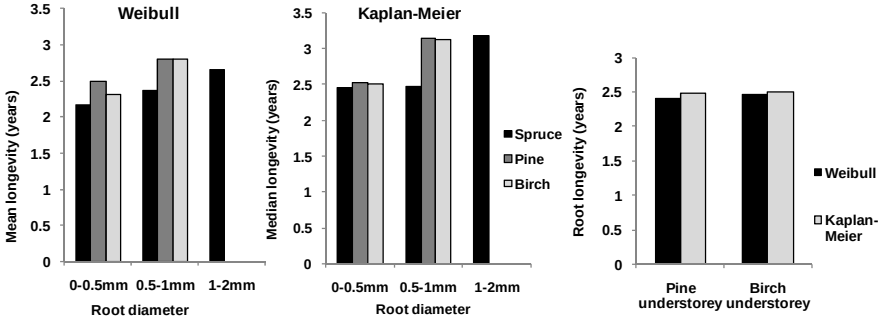

Figure 7. Estimated root longevity (years), using (left) Weibull (mean longevity) and (centre) Kaplan-Meier (median longevity) estimates for spruce, pine and birch roots sorted into different diameter classes; and (right) estimated understorey fine root longevity using Weibull (mean longevity) and Kaplan-Meier (median longevity) estimates. In the 1-2 mm fraction, sufficient data were available only for spruce.

5.2.2 Fine root turnover (Paper V)

Root lifetime distribution differed significantly between species, and estimates of fine root longevity varied from 2.17 to 3.15 years depending on species, root diameter and analysis method (Fig. 7). Comparing all fine roots, i.e. all roots with diameter 0-2 mm, pine had the highest median longevity, 3.07 years, compared with 2.53 years for birch and 2.47 years for spruce (KM method). Roots within the same species had increasing longevity with increasing diameter. Median longevity (KM) was 2.53 (pine), 2.51 (birch) and 2.45 (spruce) yr^{-1} for roots 0-0.5 mm, which was the most frequent diameter class. However, since birch had a greater proportion of

the finest roots (>80% (based on length) of all birch fine roots were in the thinnest diameter class (Fig. 8)) the proportion of the most short-lived roots was larger for birch than for pine and spruce.

For coarser fine roots (1-2 mm in diameter), it was not possible to estimate fine root longevity, partly because of few roots in that fraction (Fig. 8), but also, and more importantly, because most of those roots were still alive at the end of the study period (Fig. 8), indicating that they tend to live longer than 2-4 years (the root age range at the end of the study).

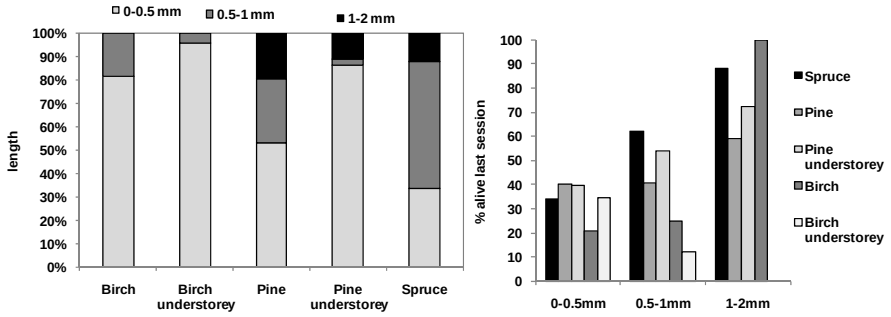

Figure 8. (Left) Diameter class, % of total fine root length per species at the end of the study and (right) fine roots, % alive at the end of the study, root length per diameter class for each species.

5.3 Carbon losses (Papers I, III, IV)

Carbon losses from the soil were estimated as leaching of DOC and loss of CO_2 through heterotrophic respiration.

5.3.1 Dissolved organic carbon and nitrogen (Papers I, III)

Dissolved organic carbon was mainly transported from the O to the B-horizon, whereas losses below the B-horizon were small for all species (Fig. 9). The DOC concentrations under the O-horizon were significantly lower in birch stands (25 mg L^{-1}) compared with pine (39 mg L^{-1}) and spruce (43 mg L^{-1}) stands. Under the B-horizon, DOC concentrations were significantly lower in birch (6 mg L^{-1}) than in pine (8 mg L^{-1}) stands, with spruce (5 mg L^{-1}) intermediate. However, since water fluxes were larger in birch stands, the relative species differences were smaller for DOC fluxes (Fig. 9) than for DOC concentrations. The lower concentrations and fluxes under the O-horizon in birch stands are probably related to the thinner O-horizons in the birch stands.

Annual water fluxes under the B-horizon were 550 mm for spruce, 690 mm for pine and 810 mm for birch. The difference in water flux is related

to differences in leaf area, which has a large influence on transpiration and interception losses and was greatest in spruce stands.

Dissolved nitrogen (DN) followed a similar distribution pattern to DOC, with fluxes decreasing with soil depth (Fig. 9). Both DOC and DN fluxes under the B-horizon were significantly lower in spruce than in pine stands. Birch had an intermediate DOC flux, but the highest DN flux, significantly different from that in spruce stands. Spruce seemed to have the ability to retain N in the system, whereas it was lost from pine and birch stands.

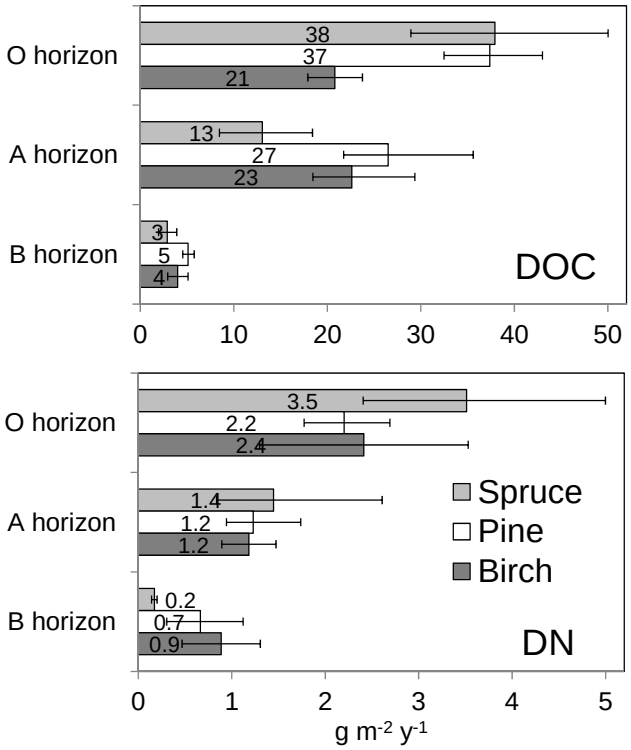

Figure 9. Fluxes of dissolved organic carbon (DOC) and dissolved nitrogen (DN) under different soil horizons. Error bars represent the 95% confidence interval (95% bootstrapped percentile interval).

The large decrease in DOC flux from the O- to B-horizon (Fig. 9) represents both C mineralisation and sorption to mineral particles. Sorption of DOC in the mineral soil is probably the main process by which DOM is retained in forest soils (Kalbitz *et al.*, 2005). Since mineral soils in spruce and pine stands had larger inflows of DOC than soils in birch stands, but similar outflows under the B-horizon, the DOC net inflow was larger in the coniferous stands. In the field study it was not possible to separate DOC of

different origins (i.e. needle *vs.* root litter). However, the incubation study, comparing DOC from different substrates at different stages of decomposition, showed that even though roots decomposed more slowly, with lower respiration and DOC flux from the columns, the proportion of DOC compared with CO_2 was larger for roots than for needles during decomposition (Fig. 10). Furthermore, the proportion of DOC was significantly larger for the seven-year-old roots compared with fresher substrates.

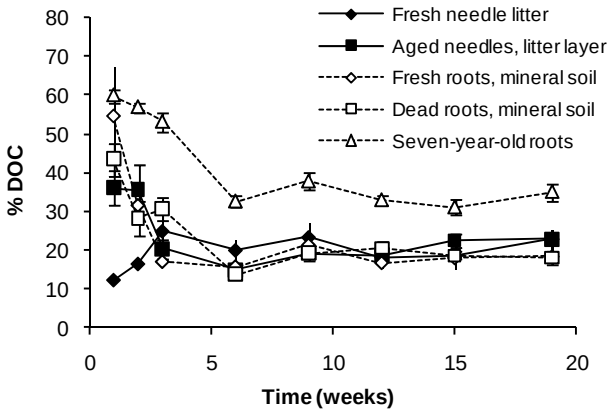

Figure 10. Percentage of dissolved organic carbon (DOC/(DOC+CO_2)×100) leached from columns containing different substrates (n=4, mean±SE).

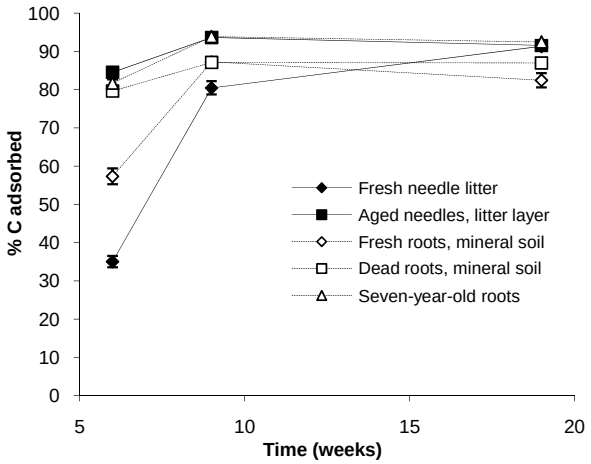

Figure 11. Sorption to ferrihydrite shown as percentage of carbon in leachate adsorbed to ferrihydrite. Pooled samples of leachate after 6 (n=6), 9 (n=5) and 19 (n=5) weeks of incubation (mean±SE).

In Sweden, most forest soils are podzolic, with the main part of SOM sequestered in the iron-rich B-horizon (Olsson *et al.*, 2009). In the incubation study, more well-decomposed litter, with higher SUVA, was more strongly sorbed to the ferrihydrite (Fig. 11).

There were no differences between species in DOC quality, expressed as SUVA, but SUVA decreased with soil depth from 4-6 L mg^{-1} m^{-1} under the O-horizon to 1-3 L mg^{-1} m^{-1} under the B-horizon (Fig. 12). A similar trend has been reported previously (e.g. Don & Schulze, 2008; Sanderman *et al.*, 2008) and attributed to additions of DOC with low SUVA at depth (Sanderman *et al.*, 2009). In the incubation study, DOC from fresh roots had higher SUVA than DOC from fresh needles, but SUVA was still significantly lower than in DOC from more well-decomposed needle and root material (Fig. 12).

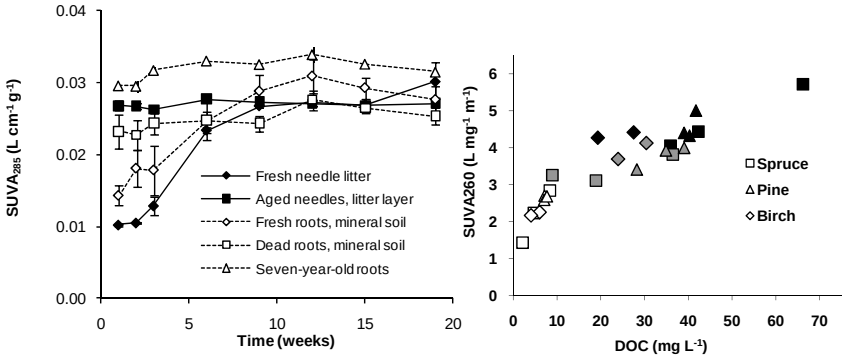

Figure 12. SUVA (ultraviolet absorbance at 285 nm divided by DOC concentration) measured in leachate from (left) the incubation study (absorbance at 285 nm) and (right) field samples from Tönnersjöheden (absorbance at 260 nm, filled black symbols represent the O-horizon, grey symbols the A-horizon and open symbols the B-horizon). Increasing SUVA indicates increasing aromaticity of DOC.

5.3.2 Heterotrophic respiration and N mineralisation (Paper IV)

Carbon mineralisation (heterotrophic respiration) rate (g^{-1} C d^{-1}), determined at 15 °C in the laboratory, was about three-fold higher in humus samples from birch stands than in those from pine and spruce stands at Tönnersjöheden. There were no significant differences between species in mineral soil samples. In soils from Kivalo, C mineralisation rate in humus was significantly lower in pine than in spruce and birch stands (Fig. 13).

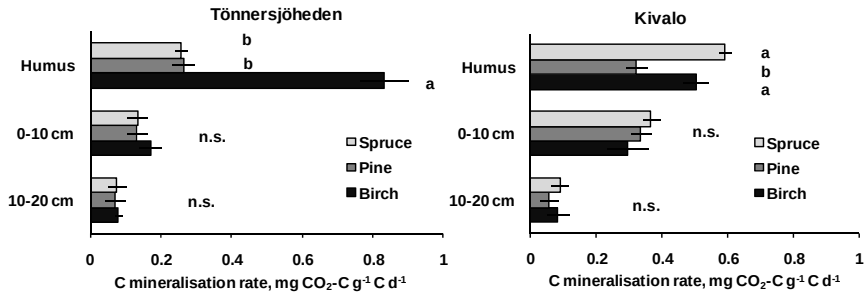

Figure 13. Mean C mineralisation rate (±SE) at 15 °C in stands of different tree species in the humus (Oe + Oa) layer and the 0–10 and 10–20 cm layers of the mineral soil at Tönnersjöheden (left) and Kivalo (right). Different letters indicate significant differences ($P<0.05$) between tree species.

At both Tönnersjöheden and Kivalo, estimated total (humus and 0-20 cm mineral soil) annual field C mineralisation was significantly higher in spruce plots than in pine plots, and C mineralisation was also higher in spruce plots than in birch plots at Tönnersjöheden (Fig. 14). 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.

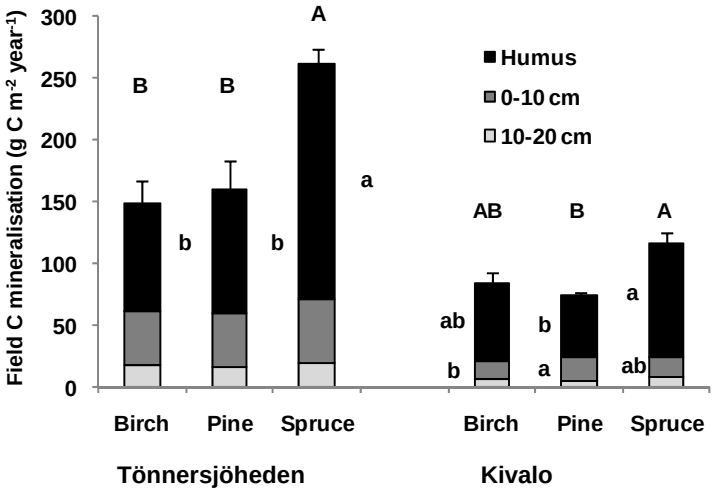

Figure 14. Estimated annual C mineralisation (±SE) in the field in stands of different tree species in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil at Tönnersjöheden (left) and Kivalo (right). Different upper-case and lower-case letters indicate significant differences ($P<0.05$) in total pools and pools of specific soil layers, respectively.

The net N mineralisation rate (g^{-1} C d^{-1}) at Tönnersjöheden was significantly higher ($P<0.05$) in birch stands than in pine and spruce stands in both the organic and 0-10 cm mineral soil layer, and tended to be so even in the 10-20 cm layer. Estimated total (humus and 0-20 cm mineral soil) field net N mineralisation at Tönnersjöheden was substantial, about 8 g N m^{-2} yr^{-1}, but there was no difference between tree species (Fig. 15). The N mineralisation rate, as well as field net N mineralisation at Kivalo, was very low and there were no differences between tree species for any soil layer (Fig. 15).

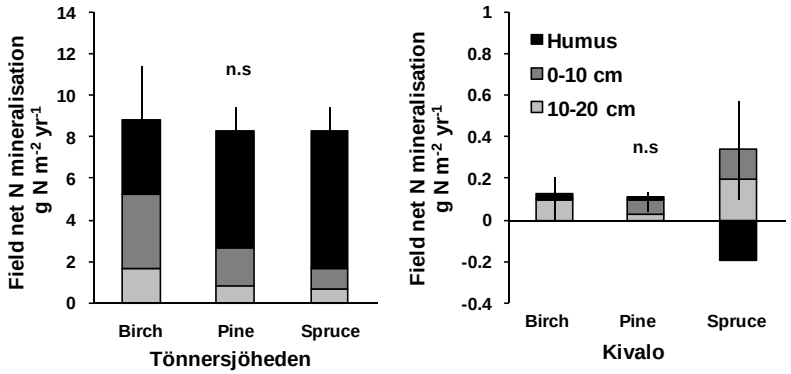

Figure 15. Field annual net N mineralisation (±SE) estimated in stands of different tree species in the humus (Oe + Oa) layer and the 0-10 and 10-20 cm layers of the mineral soil at Tönnersjöheden (left) and Kivalo (right) (note difference in scales). Different upper-case and lower-case letters indicate significant differences ($P<0.05$) in total pools and pools of specific soil layers, respectively.

5.4 Other factors affecting carbon in forest soils (Papers II, IV, V)

Many factors are closely linked to the carbon fluxes in forests. Nitrogen pools and fluxes have already been mentioned, but we also studied earthworm abundance, fungal growth, soil acidity and mineral nutrient content in soil. Other factors, not further discussed in this thesis, are e.g. forestry practices and harvest, grazing by mammals, precipitation and temperature.

5.4.1 Earthworm abundance (Paper IV)

The overall abundance of earthworms was significantly higher in birch stands than in coniferous stands. *Dendrobaena octaedra* was the most abundant earthworm species at Tönnersjöheden (Fig. 16). The abundance of

Lumbricus rubellus, which was only found in pine and birch stands, was also higher in the birch stands. Because *L. rubellus* is about 5-10 times larger than *D. octaedra*, the earthworm biomass was much higher in birch stands than in the coniferous stands.

Many studies have demonstrated the capacity of *D. octaedra* and *L. rubellus* and other detritus-feeding earthworms of the forest floor to dramatically change soil conditions if population densities increase (e.g. Frelich *et al.*, 2006; McLean & Parkinson, 2000; Saetre, 1998). Both species are litter-dwelling (epigeic), and *L. rubellis* also have some capacity to mix mineral soil with the organic horizon (epi-endogeic). Thus, the more blurred transition between the organic layer and the mineral soil in the birch plots at Tönnersjöheden agrees with the occurrence of *L. rubellus*.

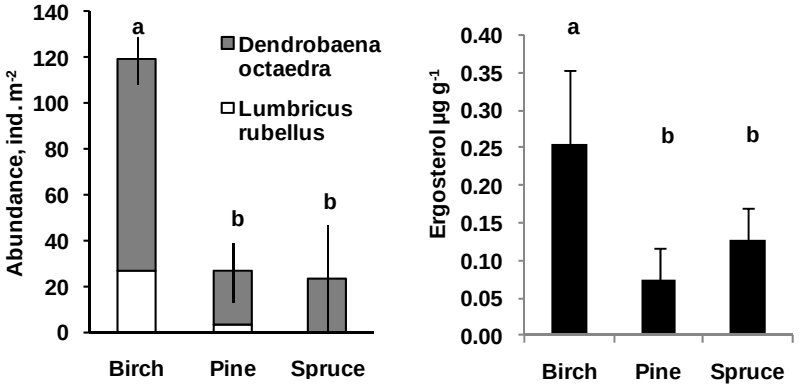

Figure 16. Abundance of earthworms in soil layers (Oi, Oe, Oa and mineral soil 0–20 cm) in stands of different tree species at Tönnersjöheden (left) and fungal biomass (µg ergosterol g^{-1} sand) in mesh bags filled with sand (n=3 spruce, pine stands, n=2 birch stands; least squares means±SE). Different letters indicate significant differences between species ($P<0.05$).

5.4.2 Fungal growth (Paper V)

Fungal biomass (ergosterol) was significantly higher in birch stands, 0.26 µg ergosterol g^{-1} sand, compared with spruce and pine stands (0.13 and 0.08 µg ergosterol g^{-1} sand, respectively) (Fig. 16).

This does not reflect the extent of mycorrhizal colonisation, but rather expresses fungal growth. Birch stands had more mycelial growth, probably due to disturbance of the soil through bioturbation. Earthworms were much more abundant in birch than in spruce and pine stands (Fig. 16). When the soil is constantly turned over, the mycelia network is disturbed, and more fast-growing fungal species are favoured (McLean & Parkinson, 2000).

5.4.3 Soil acidity and mineral nutrients (Paper II)

Birch stands had significantly higher soil pH (5.0) in the humus layer than pine (4.4) and spruce (4.1) stands, but pH in pine and spruce stands increased with soil depth and at 30 cm depth in mineral soil differences were small (Fig. 17).

Amounts of base cations (K, Ca, Mg and Na) differed significantly between species in the humus layer, but not in the mineral soil, with the largest amounts in the spruce stands and smallest in birch stands, with pine intermediate.

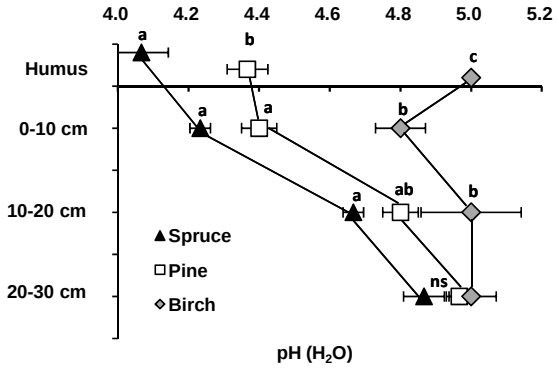

Figure 17. Differences in pH (H_20) at different soil depths (n=3 spruce, pine, n=2 birch; least squares means). Different letters indicate significant differences between species ($P<0.05$), ns = not significant.

5.4.4 Nitrogen pools and fluxes

It was not the ambition to draw up a complete N budget for the different stands, but N measurements were included in all studies (Papers I-V). Figure 18 summarises the measured N pools and fluxes at Tönnersjöheden. Ammonium and nitrification (Fig. 18) was extrapolated from data in Paper IV, assuming that the result from 30 days incubation is valid for the whole year.

The N content in tree biomass was not measured, and the amount of N in leaf litter did not differ significantly between species, but C:N ratio in litterfall differed significantly between species (birch<spruce<pine).

Spruce stands had the highest N inflow through litter and deposition and the largest N pool in soil, but the least N lost through leaching of DN (*cf.* Figs. 5, 9, 18). The spruce stands seemed to have the ability to retain N in the soil, whereas it was lost from the pine and birch stands.

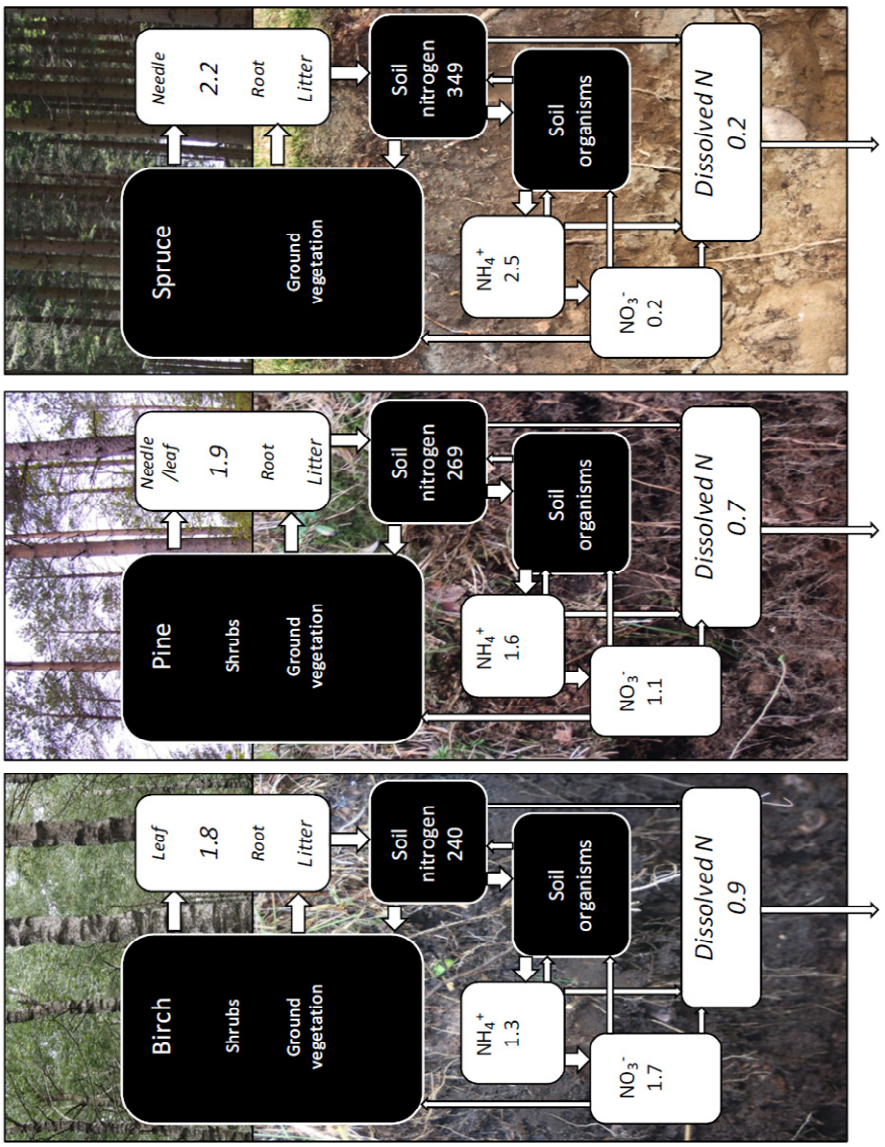

Figure 18. Estimated nitrogen pools (g N m^{-2}) and fluxes (g N m^{-2} $year^{-1}$) in birch, pine and spruce stands at Tönnersjöheden. Pools are displayed in black boxes, fluxes in white.

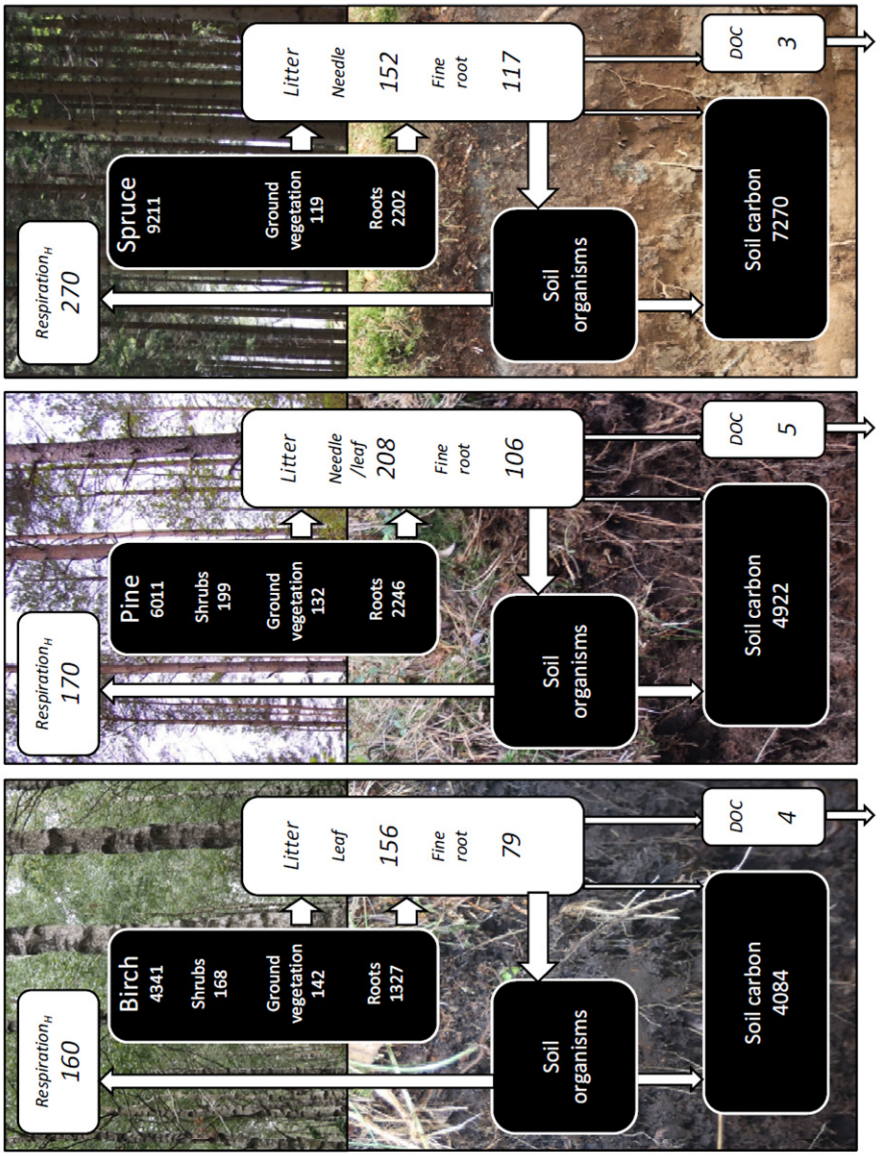

Figure 19. Estimated carbon pools (g C m^{-2}) and fluxes (g C m^{-2} $year^{-1}$) in birch, pine and spruce stands at Tönnersjöheden. Pools are displayed in black boxes, fluxes in white.

5.5 Carbon pools and fluxes

Figure 19 summarises the carbon pools and fluxes measured in Papers II-V. Soil carbon pools were smallest in birch stands at Tönnersjöheden, explained

5.5 Carbon pools and fluxes

Figure 19 summarises the carbon pools and fluxes measured in Papers II-V. Soil carbon pools were smallest in birch stands at Tönnersjöheden, explained by lower inputs of litter and faster turnover, both through lower leaf and root longevity and faster decomposition. The presence of earthworms seemed to explain a large part of the difference between birch and conifer stands. The preference of earthworms for birch litter leads to more bioturbation in the birch stands, disrupting fungal mycelia and root networks and separating litter into smaller pieces, which in turn speeds up heterotrophic respiration. Physical mixing may be the most important pathway for translocation of C from surface to deeper soil layers in birch stands, whereas DOC influx to the mineral soil is more important in pine and spruce stands.

5.5.1 How reliable are the results?

Some of the observed differences between tree species, such as those in the soil carbon pool, were large, whereas others, such as those in DOC fluxes, were small and the spatial variation was sometimes large (Fig. 19). A few comments on the reliability of the data are necessary. Some data, such as basal area (Table 1) and soil pH (Fig. 17) were measured directly and are therefore among the most reliable data in this study. Other data, such as soil C, N, base cations, earthworm abundance and litterfall, were extrapolated from collected data. These data are thus also reliable, and significant differences should represent actual differences. Some data, such as coarse root biomass and ground vegetation turnover, were estimated using data and functions from the literature. It is difficult to know how similar the stands in the present study are to those in the literature, and therefore these results are estimates.

The DOC fluxes presented here were based on modelled water fluxes. The model included specific soil parameters for each plot, as well as measured LAI, and the results should be reliable.

Soil C and N pools were estimated twice for Tönnersjöheden (Papers II and IV), with slightly different results. The analyses were carried out at laboratories with different equipment, which probably explains the discrepancy. Overall, there was a similar pattern between tree species and the conclusions did not differ.

Fine root turnover is difficult to quantify, and several methods may be used, which makes it difficult to compare results between studies (see e.g. Gaudinski *et al.*, 2010; Strand *et al.*, 2008; Metcalfe *et al.*, 2007).

Minirhizotrons have been reported to yield the most reliable root longevity and production data (Hendricks *et al.*, 2006). However, even when using minirhizotrons, there are several assumptions made that affect the results: How are dead roots defined? Should roots that disappear be included? Should roots that are still alive at the end of the study be excluded? What type of lifetime distribution analysis should be used (Kaplan-Meier, Weibull)? The differences in fine root turnover rate between tree species in this study are reliable, since we used the same assumptions for all species. Even though the exact numbers varied depending on whether KM or Weibull analysis was used, the pattern was the same for both analyses. However, when comparing the results with other studies, one important factor to take into account is that we chose to define roots as gone and not as dead, sometimes including root decomposition in the turnover. Therefore, this overestimation of root longevity by a few months should be taken into account if our results are compared with those of other studies reporting fine root longevity from birth to observed death.

5.5.2 What is missing?

It was not possible within this project to measure all major carbon pools and fluxes in the forest system. When comparing Fig. 1 and Fig. 19, some fluxes are not included in the latter, e.g. autotrophic respiration or biomass removed by harvest was not included. The main focus was on soil carbon and unfortunately some pieces of the puzzle are missing there, which is why no attempt was made to calculate a mass balance for the different species.

It would have been useful to include heterotrophic respiration from the litter layer, but unfortunately this was not possible due to difficulties when sampling. Field carbon mineralisation rates were therefore underestimated and since the tree species differed in litter quality and quantity, it is reasonable to expect differences between species in litter layer mineralisation rates.

Coarse woody debris was not included. Stumps are the largest coarse woody debris 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. Coarse woody debris can be an important long-term carbon pool, but it is difficult to quantify and the spatial variation is large.

6 Main conclusions

- Soil C fluxes and the accumulation of soil organic carbon at Tönnersjöheden differed between the three species studied, with the strongest differences in humus layers between spruce and birch stands, with pine intermediate.
- Most carbon was stored in soils in spruce stands at Tönnersjöheden, whereas birch stands had the fastest root turnover and the highest C mineralisation rate.
- Species differences were more pronounced at the southernmost site, Tönnersjöheden than at the northernmost, Kivalo.
- Species differences can be explained by differences in tree growth rate, but also by differences in decomposition. At Tönnersjöheden species differed in litter quality, carbon mineralisation, DOC fluxes and fine root turnover.

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Svensk sammanfattning

Mängden utsläpp av växthusgasen koldioxid påverkas av olika kolkällor och sänkor. Europeisk skog är en viktig kolsänka, främst genom kolinlagring i ökad trädbiomassa, men också genom att kol lagras i marken. Många olika faktorer – såsom trädtillväxt, markvegetation, det organiska materialets nedbrytningshastighet och läckage av organiskt material med markvattnet – påverkar skogens kolflöden och förråd. Olika trädslag har olika tillväxt, förnakvalitet och kvävedeposition och påverkar kolflödena på olika sätt. Med ändrad trädslagssammansättning påverkas kolförråden, vilket indirekt kan påverka klimatet. Det är därför viktigt att känna till skillnader mellan specifika trädslag.

I Sverige är gran, tall och björk de tre vanligaste trädslagen, med 41, 39 och 13 % av virkesförrådet. I södra Sverige är fördelningen lite annorlunda, med 45 % gran, 30 % tall and 11 % björk. Gran, tall och björk planteras ofta på olika typer av mark, tallen klarar sig till exempel bättre på torr, mager mark än vad granen gör. Få studier har fokuserat på skillnader mellan trädslag som växer på samma mark. Syftet med mitt doktorandprojekt har varit att jämföra kolflöden och kolförråd i närliggande gran-, tall- och björkbestånd i Halland; främst genom fältstudier vid Tönnersjöhedens försökspark i Halland (studie II, III och V), men också genom respirations- och nedbrytningsstudier i klimatkammare (studie I och IV).

Den första studien jämförde nedbrytning av granrötter och barr, genom inkubering av substraten vid konstant temperatur. Mätningar av respiration och utlakning av organiskt material gjordes regelbundet under 6 månader.

I den andra studien undersöktes skillnader i markkemiska förhållanden mellan bestånd av gran, tall och björk i Halland. Texturanalyser och geokemiska analyser säkerställde att markförutsättningarna i de olika bestånden var lika, bortsett från trädslaget. Markens kol, kväve, baskatjoner och pH mättes, men också fallförnans mängd och kvalitet samt busk- och markvegetationens utbredning.

Studie tre handlar om markvattnet. Lösligt kol och kväve i markvattnet mättes under två år med hjälp av lysimetrar i marken, och markvattenflödena modellerades.

I den fjärde studien jämfördes kol- och kvävemineralisering i jord från gran, tall och björkbestånd i Halland och i norra Finland, utanför Rovaniemi. Substraten inkuberades i klimatkammare med konstant temperatur under 30 dagar. Varje vecka mättes respiration, medan kväve mättes före och efter inkuberingen.

Studie fem jämförde finrotsomsättning i gran, tall och björkbestånd i Halland. Foton av samma rötter togs 2-4 gånger per år under 4 år. Genom att analysera bilderna och mäta förändringar, när nya rötter föddes och hur länge de levde, kunde sedan genomsnittlig livslängd av rötterna beräknas.

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Resultaten visar att det är skillnader mellan trädslagen i kolflöden och kolförråd, även om trädslagen växer på liknande mark. Produktionen var störst i granbestånden och nedbrytning, kväveutlakning och rotomsättning var störst i björkbestånden. Den här avhandlingen har gett ytterligare en pusselbit till att förstå kolcykelns komplicerade interaktioner mellan växter, markorganismer och markkemiska förhållanden. Min förhoppning är att resultaten kan användas för att förbättra framtida kolflödes-modelleringar.

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