



Differences in soil properties in adjacent stands of Scots pine, Norway spruce and silver birch in SW Sweden

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ARTICLE INFO

Article history:

Received 8 November 2010

Received in revised form 13 April 2011

Accepted 14 April 2011

Available online 10 May 2011

Keywords:

Betula pendula

Carbon

Nitrogen

Soil pH

Picea abies

Pinus sylvestris

ABSTRACT

Soil properties were compared in adjacent 50-year-old Norway spruce, Scots pine and silver birch stands growing on similar soils in south-west Sweden. The effects of tree species were most apparent in the humus layer and decreased with soil depth. At 20–30 cm depth in the mineral soil, species differences in soil properties were small and mostly not significant. Soil C, N, K, Ca, Mg, and Na content, pH, base saturation and fine root biomass all significantly differed between humus layers of different species. Since the climate, parent material, land use history and soil type were similar, the differences can be ascribed to tree species. Spruce stands had the largest amounts of carbon stored down to 30 cm depth in mineral soil (7.3 kg C m⁻²), whereas birch stands, with the lowest production, smallest amount of litterfall and lowest C:N ratio in litter and humus, had the smallest carbon pool (4.1 kg C m⁻²), with pine intermediate (4.9 kg C m⁻²). Similarly, soil nitrogen pools amounted to 349, 269, and 240 g N m⁻² for spruce, pine, and birch stands, respectively. The humus layer in birch stands was thin and mixed with mineral soil, and soil pH was highest in the birch stands. Spruce had the thickest humus layer with the lowest pH.

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1. Introduction

One of the most important decisions in temperate and boreal forestry is the choice of tree species. Tree species affect soil properties, such as soil organic matter accumulation and soil acidity, in many ways. Differences in litter quality, together with litter amounts, affect the decomposer community, decomposition and turnover of organic material, and the formation of soil organic matter (Vesterdal et al., 2008; Hobbie et al., 2010). Differences regarding yield capacity, litter amounts, fine root turnover and nutrient accumulation in biomass affect the soil acid–base status (Priha and Smolander, 1999; Nilsson et al., 2007; Vesterdal et al., 2008). Species also differ in canopy structure, affecting throughfall chemistry, dry deposition and light transmittance, which may lead to different types of understorey vegetation (Bergkvist and Folkesson, 1995; Augusto et al., 2002; De Schrijver et al., 2007; Barbier et al., 2008).

In Sweden, there are three dominant tree species: Norway spruce (*Picea abies*) with 41% of standing volume of forests, Scots pine (*Pinus sylvestris*) with 39% and birch (*Betula pendula* and *Betula pubescens*) with 13% (Anonymous, 2010a). The relative proportions in southern Sweden 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. In southern Sweden spruce has higher production rate than birch, with pine intermediate (Ekö et al., 2008; Anonymous, 2010a).

As a result of climate change, with associated higher temperatures and changes in humidity, species composition in unmanaged forests in Sweden is predicted to change, with deciduous species spreading towards the north (Koca et al., 2006). In addition, the tree species composition in managed forests may change, which in turn has the potential to change production, turnover and sequestration of carbon in vegetation and soil.

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 the 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 properties. The aim of the present study was to examine how adjacent Norway spruce, Scots pine, and silver birch stands, established on similar soils in south-west Sweden, influenced soil properties during one rotation period. At the experimental site we selected similarly aged stands with different stand density, reflecting the situation in the region, with spruce often having larger basal area per hectare than birch. This enabled a comparison of differences caused not only by species per se, but also by the differences in e.g. ground vegetation

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following the different light conditions in the stands, rather than comparing stands with same basal area.

We hypothesised that changes in soil organic matter reflect both litter production and litter quality. Specifically, we predicted that the birch stands, with lower production and different litter chemistry than the coniferous stands, would have (i) thinner humus layers and less carbon and nitrogen stored in the soil, (ii) higher soil pH and base saturation and (iii) a larger pool of exchangeable base cations.

2. Materials and methods

2.1. Study site and experimental design

The study area is located in the Tönnersjöheden Experimental Forest in south-west Sweden (56°40'–41'N, 13°03'–06'E) at 70–90 m above sea level. Mean annual air temperature was 6.4 °C and mean annual precipitation was 1053 mm for the reference period 1961–1990 (Alexandersson et al., 1991). The duration of the growing season (temperature >5 °C) is 204 days (Olsson and Staaf, 1995).

The experimental design included stands of three tree species, Norway spruce (*P. abies* (L) Karst.), Scots pine (*P. sylvestris* L.) and silver birch (*B. pendula* Roth), replicated in a block design ($n = 3$, except for birch where $n = 2$). Plot size ranged from 720 to 1296 m² (Table 1). Most plots used in the present study were established as parts of other experiments (Table 1). However, the previous treatments, concerning provenance and thinning, were not considered to have caused any bias in the present study. A survey of the Tönnersjöheden Experimental Forest by Malmström (1937) indicated that by 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 of 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 m² ha⁻¹ (Table 2). Spruce stands have the highest average basal area, 29.3 m² ha⁻¹, followed by 20.6 m² ha⁻¹ for pine and 15.4 m² ha⁻¹ for birch stands.

Understorey vegetation – 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 – 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. Total above-ground bottom and field layer biomass does not significantly differ between the main species, with 286, 263 and 237 g m⁻² for birch, pine and spruce stands. However, the distribution of different vegetation types differs, with spruce stands dominated by mosses, with no field layer vegetation, whereas birch and pine stands have a mixture of grass (mainly *Deschampsia flexuosa*), forbs, ericoid dwarf shrubs (mainly *Vaccinium vitis-idaea*, *Vaccinium myrtillus* and *Calluna vulgaris*), mosses and trees (Table 2).

The spruce plots do not have any shrub layer vegetation, whereas small trees and shrubs are common in the pine and birch stands. Shrub layer basal area is higher in pine than in birch stands in block 3, with small species differences in block 1, where shrubs are less common (Table 2). *Frangula alnus* is the most common shrub, present on all experimental plots. Other common species are *B. pendula*, *Fagus sylvatica*, *Quercus robur* and *Sorbus aucuparia*. On some plots we also found *Juniperus communis*, *Larix* spp., *P. sylvestris*, *Salix caprea* and *Malus* spp. Most shrubs are small, often with diameter at base (DAB) <1.5 cm and the majority are less than 4 m high, with a DAB <5 cm, but both birch and pine stands have few large spruce trees >10 m high. In blocks 2 and 3, where shrubs are most common, shrub layer basal area constitutes 4–8% of total stand basal area (i.e. shrub and tree layer), calculated with diameter at breast height (DBH).

2.2. Soil sampling and analyses

The soil parent material is of glacial origin (Malmström, 1937). The stoniness, to a depth of 30 cm, was measured at 25 locations in each stand and calculated according to Stendahl et al. (2009) modified from Viro (1952). A soil profile was dug at the border of each plot and the soil type was classified according to IUSS Working Group WRB (2006).

Three soil samples per plot from 30 and 70 cm depth, respectively, were taken and bulked for texture analyses, and from 70 cm depth for geochemical analyses of parent material. The purpose of the texture and geochemical analyses was to verify that all plots had similar parent material composition.

Ten samples per plot were taken in 2006 for soil chemical analyses from the humus layer and from 0–10, 10–20 and 20–30 cm depth in the mineral soil. A soil corer with 5.5 cm diameter was used for the humus layer and a soil corer with 4.5 cm diameter

Table 1
Stand establishment, year of thinning and size of studied plots.

Stand	Original experimental purpose	Year of planting	Age of seedling material	Spacing in plantation	Year of thinning	Plot size (m ²)	Soil type (WRB)
Block 1							
Silver birch	Study on tree species effects on forest production	1951	2 years	1.2 × 1.2 m	1975, 1979, 1984, 1989, 1995, 2002	900	Dystric arenosol
Scots pine	Study on tree species effects on forest production	1960	3 years	1.5 × 1.5 m	1983, 1987, 1995, 2002	750	Dystric regosol
Norway spruce	Study on tree species effects on forest production	1962	4 years	1.5 × 1.5 m	1987, 1995, 2002	720	Dystric regosol
Block 2							
Scots pine	Study on effects of spacing in plantation	1962	3 years	1.25 × 1.25 m	1979, 1984, 1989, 1995, 2002	1036	Dystric regosol
Norway spruce	Study on tree species effects on forest production	1953	2 years	1.3 × 1.3 m	1981, 1985, 1989, 1995, 2002	1015	Dystric arenosol
Block 3							
Silver birch	Study on effects of provenance	1953	2 years	1.5 × 1.5 m	1980, 1985, 1991	1296	Dystric regosol
Scots pine	Study on effects of pre-commercial thinning	1959	2 years	1.4 × 1.4 m	1986, 1991, 1997, storm damage 2005	1080	Dystric regosol
Norway spruce	Not part of a previous study	1963	4 years	1.7 × 1.7 m	1986, 1991, 1997	900	Albic podsol

Table 2

Basal area ($\text{m}^2 \text{ha}^{-1}$) of overstorey trees, measured at 130 cm (diameter breast height, DBH); and of shrub layer in birch and pine stands, measured at root collar (diameter at base, DAB) and, when applicable, at 130 cm (many shrubs were shorter than 130 cm, with no measured DBH); bottom and field layer biomass (g dw m^{-2}), sorted into grasses, forbs, ericoids, mosses and trees ($< 50 \text{ cm}$ height) ($n = 3$ spruce, pine, $n = 2$ birch, least squares means \pm SE).

	Silver birch	Scots pine	Norway spruce
<i>Basal area overstorey</i>			
Based on DBH ($\text{m}^2 \text{ha}^{-1}$)	15.4 \pm 3.5 a	20.6 \pm 1.1 ab	29.3 \pm 3.8 b
<i>Basal area shrub layer</i>			
Based on DAB ($\text{m}^2 \text{ha}^{-1}$)	1.6 \pm 0.5 n.s.	2.4 \pm 0.9	0 \pm 0
Based on DBH ($\text{m}^2 \text{ha}^{-1}$)	0.8 \pm 0.4 n.s.	0.9 \pm 0.4	0 \pm 0
<i>Total basal area</i>			
Based on DBH ($\text{m}^2 \text{ha}^{-1}$)	16.3 \pm 3.9 a	21.6 \pm 1.0 ab	29.3 \pm 3.8 b
<i>Bottom and field layer biomass</i>			
Grasses (g dw m^{-2})	157 \pm 11 a	119 \pm 35 a	0 \pm 0 b
Forbs (g dw m^{-2})	25 \pm 6 n.s.	22 \pm 8	0 \pm 0
Ericoids (g dw m^{-2})	17 \pm 15 n.s.	69 \pm 27	0 \pm 0
Mosses (g dw m^{-2})	69 \pm 12 ab	38 \pm 3 a	237 \pm 61 b
Trees (g dw m^{-2})	10 \pm 5 n.s.	15 \pm 11	0 \pm 0
Total (g dw m^{-2})	285 \pm 9 n.s.	263 \pm 19	237 \pm 61

Different letters indicate significant differences between species ($P < 0.05$), n.s. = not significant.

for the mineral soil. The litter layer was removed before sampling of the humus layer. The samples of each plot were bulked to one composite sample per horizon. Samples were stored at -20°C until preparation.

Soil samples for texture analyses of parent material were dried (40°C) and the $< 20 \text{ mm}$ fraction was sieved. Samples for parent material geochemical analyses were dried (40°C), homogenised and sieved. The $< 2 \text{ mm}$ fraction was ground in an agate mortar, dried (105°C), and 0.1 g dried sample was fused with 0.375 g lithium borate (LiBO_2), dissolved in HNO_3 and subsequently analysed using ICP-AES and ICP-QMS.

Soil samples were dried (40°C) and sieved, and the $< 2 \text{ mm}$ fraction was used for soil chemical analyses. Exchangeable acidity was determined by titration of potassium chloride extract, extracting 20 g (mineral soil) or 10 g (humus) in 100 ml potassium chloride (1 M). Exchangeable cations in the soil samples were determined by extracting 20 g mineral soil or 10 g humus in 100 ml ammonium chloride (1 M), after which the extracts were analysed by atomic emission spectrometry (ICP AS). 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} .

Total amounts of carbon and nitrogen (N) were analysed by dry combustion (CHN600, LECO). Soil pH (H_2O) was determined in a soil–water suspension (volume ratio 1:5) after shaking for 1 h and sedimentation for 2 h. In addition to chemical analyses, the water content at 105°C was determined.

The actual mass of the humus layer per unit area was calculated from a separate sequence of 15 soil cores (diameter 7.2 cm) per plot, sampled at random positions. Sampling spots located on stumps or boulders, containing no humus, were included in the total number of sampling spots. The bulk weight of the mineral soil ($< 2 \text{ mm}$) was determined by combining data on stoniness, previously described, with the bulk weight of the samples used for chemical analyses. The mass of soil data enabled determination of C, N and exchangeable cation pools in different layers, and to a depth of 30 cm in the mineral soil.

2.3. Litterfall

Litterfall was collected during three years, from April 2007 to April 2010, with nine randomly placed litter traps (0.25 m^2 , 2 m height) on each plot, emptied three times per year. Litter was dried (70°C), bulked to one composite sample per plot and sampling oc-

casation, and 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 carbon and nitrogen (N) were analysed by dry combustion (CN2000, LECO Corporation). Samples were digested in HNO_3 and HClO_4 solution. Concentrations of Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S and Zn were determined (using ICP Optima 7200 DV).

2.4. Statistical analysis

The data on the chemical characteristics of the different stands were statistically analysed using a split-plot design in blocks, with species as mainplot factor and soil layer as subplot factor. Proc MIXED in SAS 9.2 software (SAS Institute Inc., Cary, NC, USA) was used in the statistical analyses. Results are reported as significant when $P < 0.05$. Relationship between basal area and litterfall was expressed through a linear regression.

3. Results

3.1. Soil texture and geochemistry

Our results confirmed that the experimental plots have similar soil type (Table 1), texture and geochemistry (Table 3). The soil stoniness ranged from 29% to 56%, where the range was associated with block and not with treatment (Table 3). The textural differences and geochemical differences between plots within each block were small (Table 3).

Most plots showed signs of podsolisation, even though only one fulfilled all criteria for classification as a podsol. Two plots were classified as arenosols; all soils had a high percentage of sand, but most had too much coarse material ($> 40\%$) to be classified as arenosols. The remaining soils were classified as dystric regosols (Table 1).

3.2. Litterfall

Pine had a significantly larger amount of fine litterfall ($2.3 \text{ Mg ha}^{-1} \text{ year}^{-1}$) than birch ($1.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$), with spruce intermediate ($2.0 \text{ Mg ha}^{-1} \text{ year}^{-1}$) but not significantly different from either of the other two species (Table 4). When coarse litter material was included, there was no difference between pine and spruce stands (2.6 and $2.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$ respectively), whereas

Table 3

Depth of humus layer; 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 ($n = 3$ spruce, pine, $n = 2$ birch, least squares means \pm SE).

	Silver birch	Scots pine	Norway spruce
Depth of humus layer (cm)	2.1 \pm 0.1 a	4.7 \pm 0.4 b	6.7 \pm 0.2 c
Stones and boulders (%)	41.8 \pm 7.5 n.s.	42.5 \pm 3.1	39.2 \pm 4.8
Clay 30 cm depth (< 0.002 mm, %)	3 \pm 0 n.s.	4 \pm 0	5 \pm 1
Clay 70 cm depth (< 0.002 mm, %)	1 \pm 0 n.s.	1 \pm 0	2 \pm 1
Sand 30 cm depth (0.02–2 mm, %)	87 \pm 0 n.s.	87 \pm 2	83 \pm 2
Sand 70 cm depth (0.02–2 mm, %)	97 \pm 1 n.s.	96 \pm 0	93 \pm 2
CaO 70 cm depth % dw	1.82 \pm 0.07 n.s.	1.72 \pm 0.07	1.85 \pm 0.09
Fe ₂ O ₃ 70 cm depth % dw	4.21 \pm 0.14 n.s.	4.74 \pm 0.48	4.60 \pm 0.13
MgO 70 cm depth % dw	1.04 \pm 0.04 n.s.	0.97 \pm 0.09	1.06 \pm 0.02
MnO 70 cm depth % dw	0.077 \pm 0.003 n.s.	0.083 \pm 0.008	0.081 \pm 0.002

Different letters indicate significant differences between species ($P < 0.05$), n.s. = not significant.

Table 4

Amounts of elements in litterfall ($n = 3$ spruce, pine, $n = 2$ birch, least squares means \pm SE).

	Silver birch	Scots pine	Norway spruce
C (Mg ha ⁻¹ year ⁻¹)	0.657 \pm 0.128 a	1.20 \pm 0.09 b	1.01 \pm 0.12 ab
N (kg ha ⁻¹ year ⁻¹)	17.8 \pm 3.3 n.s.	19.2 \pm 2.1	22.5 \pm 1.5
C:N	37 \pm 0 a	58 \pm 2 b	45 \pm 2 c
Ca (kg ha ⁻¹ year ⁻¹)	5.27 \pm 0.80 n.s.	7.19 \pm 0.55	8.42 \pm 0.84
K (kg ha ⁻¹ year ⁻¹)	2.06 \pm 0.46 n.s.	1.96 \pm 0.23	2.54 \pm 0.22
Mg (kg ha ⁻¹ year ⁻¹)	1.88 \pm 0.27 n.s.	1.21 \pm 0.10	1.99 \pm 0.28
Mn (kg ha ⁻¹ year ⁻¹)	1.50 \pm 0.23 n.s.	1.12 \pm 0.05	1.28 \pm 0.11
P (kg ha ⁻¹ year ⁻¹)	0.780 \pm 0.040 a	0.955 \pm 0.134 a	1.41 \pm 0.07 b
S (kg ha ⁻¹ year ⁻¹)	1.25 \pm 0.23 n.s.	1.53 \pm 0.14	1.73 \pm 0.17
Al (g ha ⁻¹ year ⁻¹)	87.1 \pm 20.2 a	531 \pm 34 b	408 \pm 57 b
B (g ha ⁻¹ year ⁻¹)	19.8 \pm 3.5 n.s.	23.9 \pm 2.2	28.3 \pm 2.8
Cu (g ha ⁻¹ year ⁻¹)	16.8 \pm 5.0 n.s.	12.5 \pm 0.4	13.1 \pm 0.9
Fe (g ha ⁻¹ year ⁻¹)	88.7 \pm 20.1 a	285 \pm 7 b	308 \pm 38 b
Na (g ha ⁻¹ year ⁻¹)	169 \pm 36 a	396 \pm 27 b	454 \pm 20 b
Zn (g ha ⁻¹ year ⁻¹)	181 \pm 32 a	115 \pm 12 b	82 \pm 14 b
Litterfall (Mg ha ⁻¹ year ⁻¹)	1.2 \pm 0.2 a	2.3 \pm 0.2 b	2.0 \pm 0.2 ab

Different letters indicate significant differences between species ($P < 0.05$), n.s. = not significant.

birch had very little coarse material, with the total amount of litterfall almost equal to the fine fraction (1.2 Mg ha⁻¹ year⁻¹). There was a weak relationship ($r^2 = 0.32$) between amount of fine litterfall and overstorey basal area of the stands, with more litterfall with higher basal area (Fig. 1). When comparing only spruce stands, the correlation was strong ($r^2 > 0.99$), whereas there was no correlation between litterfall and basal area in the pine stands, which tended to have lower basal area than the spruce stands ($P = 0.060$) despite small differences in litterfall. Spruce stands, with significantly higher basal area than birch stands ($P = 0.025$), also tended to have higher litterfall. Pine stands tended to have higher litterfall per basal area than stands of the other two species.

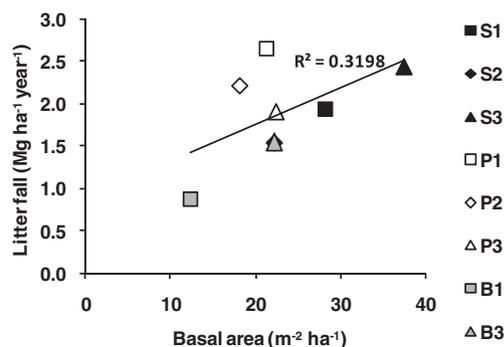


Fig. 1. Relationship between fine litterfall and overstorey basal area of stands. S = spruce, P = pine, B = birch, 1–3 = different blocks.

When comparing the amount of elements in the annual flux of fine litter per unit area, Al, C, Fe, N, Na, and P content were all significantly lower in birch stands than in spruce stands, whereas the Zn content was significantly higher in birch than in pine and spruce stands (Table 4). These differences are partly explained by differences in element concentrations. Concentrations of Al, C, Fe, Na, P and Zn in the fine litter fraction differed significantly between species (data not shown). Amounts of B, Ca, Cu, K, Mg, Mn, N and S did not significantly differ between species. However, Ca concentration was significantly lower in pine stands (8.0) compared with spruce stands (12.3), with birch (9.3) intermediate. The C:N ratio in litter significantly differed between species, with the lowest C:N ratio in birch stands (37) and the highest in pine stands (58), with spruce intermediate (45).

3.3. C and N in soil

The depth of the humus layer differed significantly between species, with the thickest humus layer in spruce stands, 6.7 cm, followed by 4.7 cm in pine stands and 2.1 cm in birch stands (Table 3). 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) (Table 5). 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 (Table 5). In the humus layer, the amount of C and N differed significantly between species, spruce > pine > birch (Fig. 2a and b). Spruce had significantly smaller amounts of C and N in all

Table 5

Amounts of C and N, and exchangeable Ca, K, Mg, Na, Al, sum of exchangeable base cations (EBC), effective cation exchange capacity (CEC_{eff}), exchangeable acidity (EA) and C:N ratio in soil, including humus layer and mineral soil 0–30 cm ($n = 3$ spruce, pine, $n = 2$ birch; least squares means \pm SE).

	Silver birch	Scots pine	Norway spruce
C (Mg ha ⁻¹)	40.8 \pm 11.2 a	49.2 \pm 7.5 a	72.7 \pm 9.9 b
N (Mg ha ⁻¹)	2.40 \pm 0.70 a	2.69 \pm 0.41 ab	3.49 \pm 0.42 b
Ca (kg ha ⁻¹)	62.0 \pm 13.8 ns	79.1 \pm 12.3	94.4 \pm 14.7
K (kg ha ⁻¹)	53.7 \pm 11.3 ns	51.3 \pm 5.6	65.6 \pm 3.8
Mg (kg ha ⁻¹)	18.1 \pm 4.1 a	25.3 \pm 3.8 a	39.6 \pm 4.5 b
Na (kg ha ⁻¹)	33.6 \pm 7.0 a	35.8 \pm 3.8 a	49.7 \pm 6.6 b
Al (kmol _c ha ⁻¹)	13.5 \pm 5.1 ns	14.0 \pm 2.6	19.7 \pm 4.6
EBC (kmol _c ha ⁻¹)	7.75 \pm 1.62 ns	8.90 \pm 1.22	11.8 \pm 1.4
CEC _{eff} (kmol _c ha ⁻¹)	45.6 \pm 13.6 ns	45.9 \pm 5.5	64.4 \pm 7.9
EA (kmol _c ha ⁻¹)	38.1 \pm 11.9 ns	37.0 \pm 4.3	52.6 \pm 6.8
C:N	17 \pm 0 a	18 \pm 0 a	20 \pm 1 b

Different letters indicate significant differences between species ($P < 0.05$), ns = not significant.

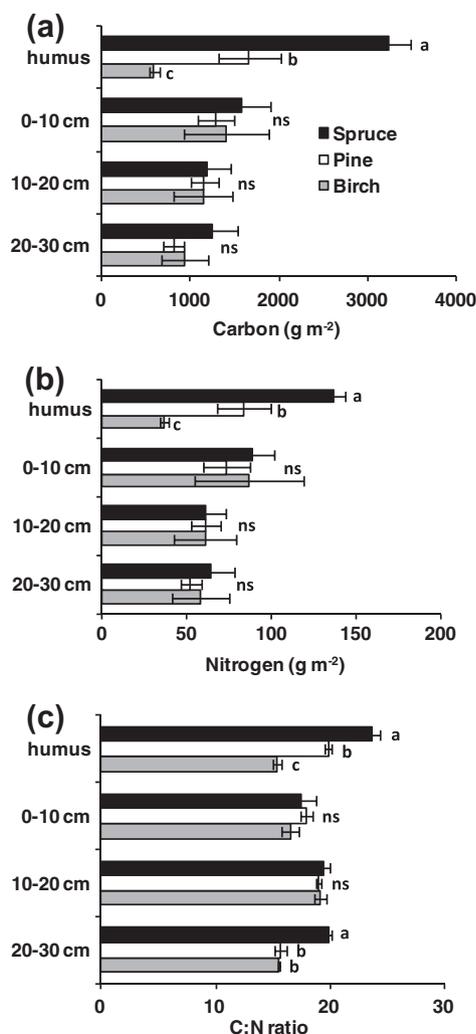


Fig. 2. Differences in (a) amount of carbon (g m^{-2}), (b) amount of nitrogen (g m^{-2}), and (c) C:N ratio at different soil depths ($n = 3$ spruce, pine, $n = 2$ birch; least squares means \pm SE). Different letters indicate significant differences between species ($P < 0.05$), ns = not significant.

mineral soil layers compared with the humus layer, pine had significantly smaller amounts of C and N in the lower part of the mineral soil compared with the humus layer, and birch had significantly smaller amount of C and N in the humus layer than in the upper part of the mineral soil. For all species, the C and N

concentrations decreased significantly with depth (data not shown).

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 (Fig. 2c). In the mineral soil only the 20–30 cm layer displayed any significant differences between species, with higher C:N ratio in soil of spruce stands than in birch and pine stands. Spruce and pine stands had significantly higher C:N ratio in the humus layer (24 and 20 respectively), compared with the 0–10 cm layer of the mineral soil (17 and 18 respectively), whereas the C:N ratio in birch stands did not differ significantly between the humus layer (15) and the 0–10 cm layer of the mineral soil (16).

3.4. Exchangeable cations and acidity in soil

Birch stands had the highest pH (H_2O), 5.0 in both humus and mineral soil, whereas pine and spruce had significantly lower pH in both the humus layer and the upper part of the mineral soil, but with pH increasing with depth (Fig. 3). Pine stands had significantly higher pH (4.4) than spruce stands (4.1) in the humus layer, whereas pH did not significantly differ between pine and spruce stands in the mineral soil. At 20–30 cm depth in mineral soil, there were no significant differences in soil pH between species.

Exchangeable acidity did not differ significantly between species (Table 5). For all species, exchangeable acidity was lowest in the humus layer ($0.06\text{--}0.6 \text{ mol}_c \text{ m}^{-2}$) and highest in the 0–10 cm mineral soil layer ($1.7\text{--}2.0 \text{ mol}_c \text{ m}^{-2}$) and decreased with depth in the mineral soil.

Spruce stands had significantly larger exchangeable Mg and Na pools for the whole soil profile (to 30 cm depth) than birch, with pine intermediate (Table 5). Spruce stands also tended to have the largest CEC_{eff} and amounts of exchangeable Ca and K, although these differences were not significant (Table 5). In the humus layer, spruce stands had significantly larger exchangeable K, Ca, Mg and Na pools than pine and birch stands (Fig. 4). The exchangeable base cation pool in the soil was larger in spruce stands compared with birch ($P = 0.054$). Pine stands tended to have larger exchangeable K, Ca, Mg and Na pools than birch in the humus layer, although the difference was only significant for Ca (Fig. 4b) and Mg (Fig. 4c). In spruce and pine stands, the base cation pool decreased with depth, except for Na, which increased with depth in pine stands and showed no significant differences with depth in spruce stands (Fig. 4d). In birch stands, differences with depth were small and not significant, except for Na, which increased with depth. Base saturation in the humus layer was significantly higher in birch (79%) than in spruce stands (52%), with pine intermediate (70%),

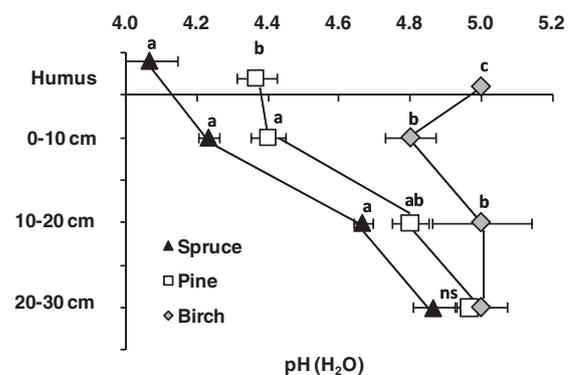


Fig. 3. Differences in pH (H_2O) at different soil depths ($n = 3$ spruce, pine, $n = 2$ birch; least squares means). Different letters indicate significant differences between species ($P < 0.05$), ns = not significant.

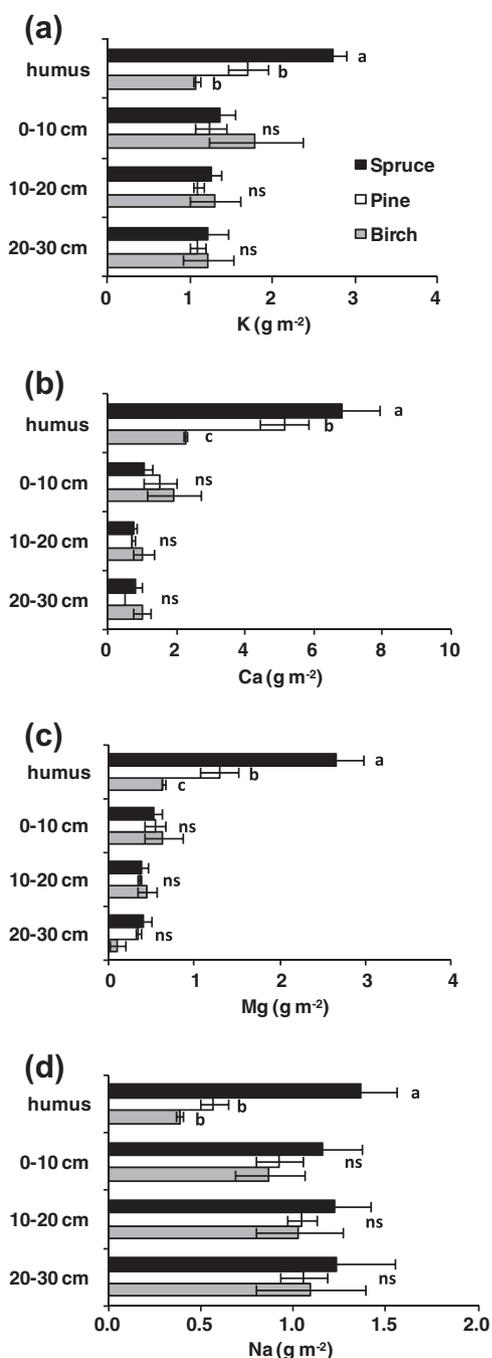


Fig. 4. Differences in amount of base cations for (a) potassium, (b) calcium, (c) magnesium, and (d) sodium at different soil depths ($n = 3$ spruce, pine, $n = 2$ birch; least squares means \pm SE). Different letters indicate significant differences between species ($P < 0.05$), ns = not significant.

whereas there were no significant differences between species in the mineral soil (Fig. 5). Aluminium content ($\text{mol}_c \text{m}^{-2}$) did not differ significantly between the species (Table 5). However, for all species there were significantly smaller amounts of Al in the humus layer ($0.002\text{--}0.08 \text{ mol}_c \text{m}^{-2}$) compared with the upper part of the mineral soil ($0.6\text{--}0.8 \text{ mol}_c \text{m}^{-2}$).

4. Discussion

The impact of tree species on soil properties is the result of interactions between the trees and the different components of

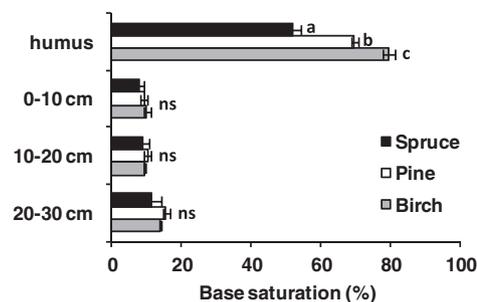


Fig. 5. Differences in base saturation (%) at different soil depths ($n = 3$ spruce, pine, $n = 2$ birch; least squares means \pm SE). Different letters indicate significant differences between species ($P < 0.05$), ns = not significant.

the ecosystem (Binkley and Giardina, 1998). Tree species affect soil properties in different ways, e.g. by chemical differences in above- and below-ground litter, differences in root activity and changes in microclimate under the tree cover, changing the understory vegetation. Our overall conclusion is that for pine, spruce and birch stands in southern Sweden, one rotation period is enough to generate clear differences in soil properties. Textural differences and geochemical differences between plots within each block were small (Table 3), and justified the attribution of observed stand differences in other soil properties to tree species.

4.1. C, N and organic matter

The differences in soil carbon pool between stands of different species (Fig. 2a), given the similar climate and parent material, can be explained by differences in production and decomposition rates. Spruce has a higher production rate than birch in this part of Sweden, with pine intermediate (Ekö et al., 2008; Anonymous, 2010a). In the present study, production and decomposition were not directly measured, but differences in basal area (Table 2) reflected differences in production, while the thinner humus layer (Table 3) and the smaller total carbon pool (Table 5) indicated faster decomposition in the birch stands compared with the spruce and pine stands.

The higher production rate in the spruce stands, manifested as differences in basal area (Table 2), was not directly reflected in litter production (Fig. 1), as pine and spruce stands did not differ in litter production, even though pine tended to have lower basal area than spruce (Table 4). One explanation for this is differences in needle longevity, as pine needle longevity is usually around 2 years, compared with 6 years for spruce needles (Reich et al., 1996), leading to the same needle litter production in pine and spruce stands even though spruce stands had larger canopies. Another explanation is the different amount of understory vegetation. Understorey trees, which were not included in the overstorey tree basal area (Table 2), contributed to litter production in the pine and birch stands, but were absent in the spruce stands. Differences in C and N content may also be explained by differences in below-ground production. Kleja et al. (2008) showed that root litter production in spruce forests can be of the same magnitude as above-ground litter production.

A higher decomposition rate of birch foliage compared to Scots pine and Norway spruce foliage (Mikola, 1960; Palviainen et al., 2004) may have contributed to the difference in soil organic matter pools. Palviainen et al. (2004) reported larger mass losses in silver birch and Scots pine leaf and root litter compared with Norway spruce needle and root litter in Finland. They also found that differences between birch and pine were small after three years of decomposition. Slower decomposition of Norway spruce litter can be explained by higher lignin content, although lignin concen-

trations vary within species. According to Johansson (1995) lignin content of Norway spruce needles was 32 %, 26 % and 28 % in Norway spruce, Scots pine and silver birch foliage, respectively. Berg and Meentemeyer (2002) found higher lignin concentrations in conifer needles than in birch leaves, but Reich et al. (2005) found higher lignin contents in silver birch than in pine and spruce. Furthermore, decomposition in birch stands is often enhanced by the presence of earthworms, mixing the soil and increasing C and N mineralisation (Saetre, 1998).

The litter quality and mineralisation rate differ between deciduous and coniferous species (e.g. Krankina et al., 1999; Polyakova and Billor, 2007; Menyailo, 2009) and also between pine and spruce (Stendahl et al., 2010). Field layer vegetation can be an important contributor to the litter layer, sometimes making up half the total litter production (Stålfelt, 1960). In the present study, the field and bottom layer in the birch and pine stands is dominated by grass, shrubs, ericoid plants and ferns, whereas the forest floor in the spruce stands is covered with mosses (Table 2), with a lower litter quality and decomposition rate (Turetsky et al., 2010). This is consistent with the lack of field layer in 40% of spruce plots in southern Sweden reported by Stendahl et al. (2010). When including the contribution of the field layer vegetation to litter production, the litter fall in the birch stands may have been of the same magnitude as that in the spruce stands (Table 4).

The thicker humus layer observed in spruce stands in the present study (Table 3) is consistent with findings in other studies (e.g. Priha, 1999; Smolander et al., 2005) and may explain observed differences in C stocks between species (Table 5). Our results are also in agreement with a soil survey of 30 forest sites in Finland (Liski and Westman, 1995) and an analysis of soil C data from the Swedish National Forest Soil Inventory (Stendahl et al., 2010). However since they included stands with different background, they were unable to distinguish between differences in species composition and differences in soil parent material composition. In the present study, there were more obvious species differences in C pools in the humus layer than in the mineral soil. In spruce stands, the humus layer contained 44% of the total carbon stock down to 30 cm depth in mineral soil (3.2 kg C m^{-2}), whereas the humus layer in the birch stands only contained 15% of total carbon stock (0.6 kg C m^{-2}), with pine intermediate (34%, 1.7 kg C m^{-2}). These numbers are consistent with the 2.8 kg C m^{-2} in the humus layer (35% of total C stock to a depth of 50 cm) reported for Swedish pod-sols by Olsson et al. (2009).

One explanation for the differences between species in carbon spatial distribution (Fig. 2a) is variations in root distribution. Root growth affects the vertical distribution of soil organic carbon, and the correlation is strongest in the upper part of the soil (Jobbágy and Jackson, 2000). Coniferous forests, with shallow root systems, tend to accumulate more soil organic matter in the forest floor and less in the mineral soil compared with deciduous species (Jandl et al., 2007).

The different amounts of soil nitrogen in spruce and birch stands, amounting to approximately $1000 \text{ kg N ha}^{-1}$, corresponds to an annual net difference in soil nitrogen accumulation rate of $20 \text{ kg ha}^{-1} \text{ year}^{-1}$ during a 50 year stand age. In addition, differences in basal area between, in particular, spruce and birch stands, suggest higher nitrogen accumulation in spruce biomass, which would add further to the discrepancy in total nitrogen pools between the birch and the spruce stands. Higher deposition of nitrogen in coniferous forests compared to deciduous may partly explain this difference. Nitrogen deposition is currently high, $> 10 \text{ kg ha}^{-1} \text{ year}^{-1}$ (Karlsson et al., 2010) in south-west Sweden, where the study site is located. A Swedish study reports 1.5–3 times higher total deposition (throughfall + stemflow) of $\text{NH}_4\text{-N}$, $\text{NO}_3\text{-N}$ and $\text{SO}_4\text{-S}$ in spruce canopies compared with birch and beech canopies (Bergkvist and Folkesson, 1995). Coniferous stands – which are

often taller than deciduous stands, with higher leaf area index and longer foliage longevity – usually intercept more nitrogen and sulphur as dry deposition than deciduous species (Augusto et al., 2002; De Schrijver et al., 2007). It is likely that differences in soil nitrogen storage were also caused by differences in decomposition and nitrogen turnover rates. Nitrification is linked to C:N ratio, with higher nitrification rate with lower C:N ratio (e.g. Andersson et al., 2002; Ross et al. 2009) suggesting higher nitrification in the birch stands. Ross et al. (2009) also found a correlation to proportion of coniferous species, with less nitrification in conifer dominated stands than in broadleaf stands. An additional cause to the different nitrogen accumulation rates could therefore be a greater nitrate leaching from the birch stands compared to the coniferous stands. However, even with large differences in N deposition and leaching, part of the nitrogen is still unaccounted for and further studies are needed to explain this difference.

The low humus layer C:N ratio in birch stands compared with conifer stands (Fig. 2c) was expected, as birch litter C:N ratio was also lower (Table 4). The C:N ratio is used to describe litter quality, and deciduous species often have a lower C:N ratio than pine and spruce (Mikola, 1985; Priha and Smolander, 1999; Smolander et al., 2005; Menyailo, 2009). Similarly, North American studies have shown that an increased admixture of foliage litter from deciduous trees with coniferous litters decrease the overall C:N ratio of the litter (Sanborn, 2001; Polyakova and Billor, 2007).

4.2. Soil acidity and mineral nutrients

Tree species can influence the acid–base status of soils in different ways. Firstly, qualitative differences in the acid–base status of soils between tree species may develop due to differences in litter quality (degradability) and base content of the litter, and differences in litter quality may also influence the composition of the decomposer communities. Secondly, quantitative differences can develop when a species with faster growth rate and faster nutrient accumulation rate accumulates more excess cations (compared with anion uptake) in biomass, leading to greater soil acidification (e.g. Nilsson et al., 1982). Another quantitative effect may result from differences in canopy structure, in particular differences between deciduous and evergreen trees, due to different capacities to intercept dry deposition, e.g. acidifying ammonium and sulphate deposition, as well as base cations (De Schrijver et al., 2007). Thirdly, species, with dissimilar rooting patterns, may differ in uptake of nutrients from subsoils. Deeply rooted tree species are often assumed to pump cation nutrients from deeper soil horizons and depositing them in litter at soil surface. However, these effects are poorly estimated (Binkley, 1995).

In the present study, we found that pH in the humus layer and upper part of the mineral soil was higher in the birch stands than in the coniferous stands (Fig. 3). In addition, base saturation followed the same pattern as pH, with significantly higher base saturation in birch stands than in spruce stands, with pine intermediate (Fig. 5). These effects, which account for the qualitative differences in the acid–base status of the uppermost soil layers, are consistent with those reported in many other studies comparing the soil status of different stands. For example, the Swedish Survey of Forest Soils and Vegetation (Nilsson et al., 2007) reported an average pH in the humus layer of 4.16, 3.75 and 3.87 for Swedish birch, pine and spruce stands, respectively. Several other studies have shown higher pH in humus layers of deciduous forests in pure stands or in admixtures compared with coniferous forests (e.g. Hallbäck and Tamm, 1986; Brandtberg et al., 2000; Hagen-Thorn et al., 2004; Oostra et al., 2006), and . Differences in pH between pine and spruce stands are often small (e.g. Smolander and Kitunen, 2002) and even though pine stands often have a lower soil pH than spruce stands (e.g. Reich et al., 2005; Nilsson et al., 2007), the

opposite, as in our study, has also been reported (e.g. Priha and Smolander, 1999). Other studies have also shown that stands of deciduous species often have a higher base saturation than conifer stands (e.g. Reich et al., 2005; Nilsson et al., 2007). The relatively high base saturation in the pine stands in the present study may have been an effect of the greater abundance of deciduous trees, shrubs and grasses in the understorey vegetation (Table 2).

A possible explanation to the differences in the soil chemistry may be composition of the litter (Table 4). Aluminium content (Table 4) and Al concentration (data not shown) in litter were significantly lower in birch stands with high soil pH (Fig. 3) than in pine and spruce stands. This was expected, since Al is more soluble at lower pH and only small amounts of soluble Al tend to be present above pH 5.2 (Barber, 1995).

Differences in canopy structure also have the potential to influence soil pH. Bergkvist and Folkesson (1995) reported 2–8 times higher dry-deposited acidity (H^+) in spruce canopies than in deciduous. Even though most of the acidity is neutralised by the foliage, dry-deposited acidity can explain part of the difference in soil pH between species. Nilsson et al. (2007) suggest that a larger deposition of acid substances in spruce stands in south-west Sweden evens out the pH differences in humus layers under pine and spruce stands in the region.

Our prediction that the exchangeable base cation pools in the soil would be ranked in the order birch > pine > spruce, due to expected greater tree biomass and nutrient accumulation in the spruce stand, was not supported by the results. Instead, the reverse ranking between species was observed for the base cations, with lower exchangeable cation pools (Table 5) in the birch stands than in the spruce stands. We can only speculate about the causes for these results. Lower dry deposition of base cations in birch forests could partly account for the smaller soil base cation pools (Bergkvist and Folkesson, 1995). However, the possibility cannot be excluded that more rapid weathering rates and lower leaching losses in the spruce stands compared with the birch stands have contributed to the different exchangeable base cation pools. Higher leaching of base cations may have occurred in companion with potentially higher nitrate leaching in birch stands. The coniferous stands had a higher content of soil organic matter and higher cation exchange capacity, suggesting a higher flux of base cations to the soil through litter fall, as well as a higher retention capacity due to the higher cation exchange capacity. Our results indicate that choice of tree species may have an impact on soil base cation pools in the same order of magnitude as the impact of harvesting intensity. Akselsson et al. (2007) showed that whole-tree harvesting, which is increasing in Sweden due to growing interest in bio-fuels, reduces nutrient pools compared to stem-harvesting.

The exchangeable pools of cations in the present study were of similar magnitude to other observations of cation pools at Norway spruce sites in the Tönnersjöheden forest (Olsson et al., 1996). Furthermore, the forest soils of glaci-fluvial origin in this region tend to have low exchangeable Ca pools compared with those in other parts of Sweden (Anonymous, 2010b). In this respect, the lower exchangeable pool of base cations in birch stands compared with spruce stands ($P = 0.054$) indicates a lower acid neutralising capacity (ANC) in birch compared with spruce stands. In conclusion, our results indicate that birch stands, compared with spruce stands in particular, produce less acid soil organic matter but also result in lower ANC and available pools of base cation nutrients.

4.3. Conclusions

Our results show that less than one rotation period is enough for clear differences to emerge in many soil properties, particularly in the humus layer, between birch, pine and spruce stands growing on similar soils. Some of our hypotheses were confirmed, with

higher soil pH and base saturation and thinner humus layers in birch stands and less carbon and nitrogen stored in the soil compared with pine and spruce stands. However, our prediction of a larger pool of exchangeable base cations in birch stands was rejected, since soil exchangeable base cation storage tended to be larger in spruce stands than birch, despite larger basal area in the spruce stands. Our study separates the effect of tree species on soil properties from confounding effects such as soil texture, geochemistry and climate. Our results are in agreement with previous findings on correlations between dominant species and soil properties. Spruce forests seem to sequester more soil carbon than pine and birch forests; however, this is connected with a lower soil pH and base saturation.

Acknowledgements

Thanks to personnel at Tönnersjöheden Experimental Forest for helping collect data and to Tomas Grönqvist for laboratory assistance. The study was originally initiated by Professor Hooshang Majdi, deceased 2007. This research was supported by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning.

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