

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

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## 15 **Abstract**

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

30

31

## 32 **Keywords**

33 *Betula pendula*, carbon, nitrogen, soil pH, *Picea abies*, *Pinus sylvestris*

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## 35 **1. Introduction**

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

46 In Sweden, there are three dominant tree species: Norway spruce (*Picea abies*) with  
47 41% of standing volume of forests, Scots pine (*Pinus sylvestris*) with 39% and birch (*Betula*  
48 *pendula* and *B. pubescens*) with 13% (Anonymous, 2010a). The relative proportions in  
49 southern Sweden are 45% spruce, 30% pine and 11% birch and this region tends to have a  
50 higher percentage of deciduous species, 25% compared with 17-19% in northern Sweden. In  
51 southern Sweden spruce has higher production rate than birch, with pine intermediate (Ekö *et*  
52 *al.*, 2008; Anonymous, 2010a).

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

58 Although it is well known that soil properties differ between stands of different  
59 species, few studies have been able to separate the effect of species on soil properties from the  
60 confounding effects of soil properties on the type of stand. Specifically, there is a lack of  
61 studies that experimentally compare the influence of the three dominant tree species in  
62 southern Sweden on soil properties. The aim of the present study was to examine how  
63 adjacent Norway spruce, Scots pine and silver birch stands, established on similar soils in  
64 south-west Sweden, influenced soil properties during one rotation period. At the experimental  
65 site we selected similarly aged stands with different stand density, reflecting the situation in  
66 the region, with spruce often having larger basal area per hectare than birch. This enabled a  
67 comparison of differences caused not only by species per se, but also by the differences in e.g.

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

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

75

## 76 **2. Materials and methods**

### 77 *2.1. Study site and experimental design*

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

83 The experimental design included stands of three tree species, Norway spruce (*Picea*  
84 *abies* (L) Karst.), Scots pine (*Pinus sylvestris* L.) and silver birch (*Betula pendula* Roth),  
85 replicated in a block design (n=3, except for birch where n=2). Plot size ranged from 720 to  
86 1296 m<sup>2</sup> (Table 1). Most plots used in the present study were established as parts of other  
87 experiments (Table 1). However, the previous treatments, concerning provenance and  
88 thinning, were not considered to have caused any bias in the present study. A survey of the  
89 Tönnersjöheden Experimental Forest by Malmström (1937) indicated that by 1890, blocks 1  
90 and 2 in the present study area were heather moorland with some admixture of pine and birch,  
91 whereas block 3 was a sparse birch forest with admixture of pine. By 1930, blocks 1 and 2  
92 consisted of dense stands dominated by Norway spruce with admixture of Scots pine, whereas  
93 silver birch dominated in block 3. The present stands of the study area were established in  
94 1951-1963 and the basal area of the established overstorey trees, measured in 2009/2010,  
95 varies from 12.3 to 37.5 m<sup>2</sup> ha<sup>-1</sup> (Table 2). Spruce stands have the highest average basal area,  
96 29.3 m<sup>2</sup> ha<sup>-1</sup>, followed by 20.6 m<sup>2</sup> ha<sup>-1</sup> for pine and 15.4 m<sup>2</sup> ha<sup>-1</sup> for birch stands.

97 Understorey vegetation – defined as bottom and field layer vegetation, shrubs and  
98 trees other than the dominant tree species layer, including large trees of species other than the  
99 dominant species and also small trees of the dominant species – was divided into two groups;  
100 bottom and field layer, defined as vegetation <50 cm height, and shrub layer, > 50 cm height.  
101 The bottom and field layer was further subdivided into grasses, forbs, ericoids, mosses and  
102 tree seedlings. Total above-ground bottom and field layer biomass does not significantly  
103 differ between the main species, with 286 g m<sup>-2</sup>, 263 g m<sup>-2</sup> and 237g m<sup>-2</sup> for birch, pine and  
104 spruce stands. However, the distribution of different vegetation types differs, with spruce  
105 stands dominated by mosses, with no field layer vegetation, whereas birch and pine stands  
106 have a mixture of grass (mainly *Deschampsia flexuosa*), forbs, ericoid dwarf shrubs (mainly  
107 *Vaccinium vitis-idaea*, *V. myrtillus* and *Calluna vulgaris*), mosses and trees (Table 2).

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

## 119 2.2. Soil sampling and analyses

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

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

128 Ten samples per plot were taken in 2006 for soil chemical analyses from the humus  
129 layer and from 0-10 cm, 10-20 cm and 20-30 cm depth in the mineral soil. A soil corer with  
130 5.5 cm diameter was used for the humus layer and a soil corer with 4.5 cm diameter for the  
131 mineral soil. The litter layer was removed before sampling of the humus layer. The samples of  
132 each plot were bulked to one composite sample per horizon. Samples were stored at -20 °C  
133 until preparation.

134 Soil samples for texture analyses of parent material were dried (40 °C) and the <20  
135 mm fraction was sieved. Samples for parent material geochemical analyses were dried (40  
136 °C), homogenised and sieved. The <2 mm fraction was ground in an agate mortar, dried (105  
137 °C), and 0.1 g dried sample was fused with 0.375 g lithium borate (LiBO<sub>2</sub>), dissolved in  
138 HNO<sub>3</sub> and subsequently analysed using ICP-AES and ICP-QMS.

139 Soil samples were dried (40 °C) and sieved, and the <2 mm fraction was used for soil  
140 chemical analyses. Exchangeable acidity was determined by titration of potassium chloride

141 extract, extracting 20 g (mineral soil) or 10 g (humus) in 100 ml potassium chloride (1M).  
142 Exchangeable cations in the soil samples were determined by extracting 20 g mineral soil or  
143 10 g humus in 100 ml ammonium chloride (1M), after which the extracts were analysed by  
144 atomic emission spectrometry (ICP AS). Effective cation exchange capacity ( $CEC_{eff}$ ) was  
145 determined as the sum of the extractable amounts of  $H^+$ ,  $Na^+$ ,  $K^+$ ,  $Ca^{2+}$ ,  $Mg^{2+}$  and  $Al^{3+}$  at soil  
146 pH. Base saturation was calculated as the equivalent sum of base cations (Ca, Mg, K, and Na)  
147 divided by  $CEC_{eff}$ .

148 Total amounts of carbon and nitrogen (N) were analysed by dry combustion  
149 (CHN600, LECO). Soil pH ( $H_2O$ ) was determined in a soil-water suspension (volume ratio  
150 1:5) after shaking for 1 h and sedimentation for 2 h. In addition to chemical analyses, the  
151 water content at 105 °C was determined.

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

### 159 *2.3. Litterfall*

160 Litterfall was collected during three years, from April 2007 to April 2010, with 9  
161 randomly placed litter traps (0.25 m<sup>2</sup>, 2 m height) on each plot, emptied 3 times per year.  
162 Litter was dried (70 °C), bulked to one composite sample per plot and sampling occasion, and  
163 sorted into two fractions, with cones and twigs with a diameter larger than 1 cm separated  
164 from the rest of the material. Both fractions were weighed and the finer fraction was further  
165 analysed. Total amounts of carbon and nitrogen (N) were analysed by dry combustion  
166 (CN2000, LECO Corporation). Samples were digested in  $HNO_3$  and  $HClO_4$  solution.  
167 Concentrations of Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S and Zn were determined (using ICP  
168 Optima 7200 DV).

### 169 *2.4. Statistical analysis*

170 The data on the chemical characteristics of the different stands were statistically  
171 analysed using a split-plot design in blocks, with species as mainplot factor and soil layer as  
172 subplot factor. Proc MIXED in SAS 9.2 software (SAS Institute Inc., Cary, NC, USA) was

173 used in the statistical analyses. Results are reported as significant when  $P < 0.05$ . Relationship  
174 between basal area and litterfall was expressed through a linear regression.

175



## 176 **3. Results**

### 177 *3.1 Soil texture and geochemistry*

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

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

### 186 *3.2. Litterfall*

187 Pine had a significantly larger amount of fine litterfall (2.3 Mg ha<sup>-1</sup> year<sup>-1</sup>) than  
188 birch (1.2 Mg ha<sup>-1</sup> year<sup>-1</sup>), with spruce intermediate (2.0 Mg ha<sup>-1</sup> year<sup>-1</sup>) but not significantly  
189 different from either of the other two species (Table 4). When coarse litter material was  
190 included, there was no difference between pine and spruce stands (2.6 and 2.5 Mg ha<sup>-1</sup> year<sup>-1</sup>  
191 respectively), whereas birch had very little coarse material, with the total amount of litterfall  
192 almost equal to the fine fraction (1.2 Mg ha<sup>-1</sup> year<sup>-1</sup>). There was a weak relationship ( $r^2=0.32$ )  
193 between amount of fine litterfall and overstorey basal area of the stands, with more litterfall  
194 with higher basal area (Figure 1). When comparing only spruce stands, the correlation was  
195 strong ( $r^2>0.99$ ), whereas there was no correlation between litterfall and basal area in the pine  
196 stands, which tended to have lower basal area than the spruce stands ( $P=0.060$ ) despite small  
197 differences in litterfall. Spruce stands, with significantly higher basal area than birch stands  
198 ( $P=0.025$ ), also tended to have higher litterfall. Pine stands tended to have higher litterfall per  
199 basal area than stands of the other two species.

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

208 The C:N ratio in litter significantly differed between species, with the lowest C:N ratio in  
209 birch stands (37) and the highest in pine stands (58), with spruce intermediate (45).

### 210 *3.3. C and N in soil*

211 The depth of the humus layer differed significantly between species, with the thickest  
212 humus layer in spruce stands, 6.7 cm, followed by 4.7 cm in pine stands and 2.1 cm in birch  
213 stands (Table 3). The total soil carbon pool (humus layer and 0-30 cm mineral soil) was  
214 significantly larger in spruce stands ( $7270 \text{ g m}^{-2}$ ) than in pine ( $4922 \text{ g m}^{-2}$ ) and birch stands  
215 ( $4084 \text{ g m}^{-2}$ ) (Table 5). Soil nitrogen followed the same distribution pattern as soil carbon.  
216 Total amount of N was significantly larger in spruce stands ( $349 \text{ g m}^{-2}$ ) than in birch stands  
217 ( $240 \text{ g m}^{-2}$ ), with pine ( $269 \text{ g m}^{-2}$ ) intermediate (Table 5). In the humus layer, the amount of C  
218 and N differed significantly between species, spruce>pine>birch (Figure 2a and b). Spruce  
219 had significantly smaller amounts of C and N in all mineral soil layers compared with the  
220 humus layer, pine had significantly smaller amounts of C and N in the lower part of the  
221 mineral soil compared with the humus layer, and birch had significantly smaller amount of C  
222 and N in the humus layer than in the upper part of the mineral soil. For all species, the C and  
223 N concentrations decreased significantly with depth (data not shown).

224 Weighted average C:N ratio for the entire profile, i.e. the ratio between total amount of  
225 C and N in the profile, was significantly lower for birch (17) and pine stands (18) than for  
226 spruce stands (20), with a similar pattern for the humus layer (Figure 2c). In the mineral soil  
227 only the 20-30 cm layer displayed any significant differences between species, with higher  
228 C:N ratio in soil of spruce stands than in birch and pine stands. Spruce and pine stands had  
229 significantly higher C:N ratio in the humus layer (24 and 20 respectively), compared with the  
230 0-10 cm layer of the mineral soil (17 and 18 respectively), whereas the C:N ratio in birch  
231 stands did not differ significantly between the humus layer (15) and the 0-10 cm layer of the  
232 mineral soil (16).

### 233 *3.4. Exchangeable cations and acidity in soil*

234 Birch stands had the highest pH ( $\text{H}_2\text{O}$ ), 5.0 in both humus and mineral soil, whereas  
235 pine and spruce had significantly lower pH in both the humus layer and the upper part of the  
236 mineral soil, but with pH increasing with depth (Figure 3). Pine stands had significantly  
237 higher pH (4.4) than spruce stands (4.1) in the humus layer, whereas pH did not significantly  
238 differ between pine and spruce stands in the mineral soil. At 20-30 cm depth in mineral soil,  
239 there were no significant differences in soil pH between species.

240 Exchangeable acidity did not differ significantly between species (Table 5). For all  
241 species, exchangeable acidity was lowest in the humus layer ( $0.06\text{-}0.6 \text{ mol}_c \text{ m}^{-2}$ ) and highest  
242 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  
243 soil.

244 Spruce stands had significantly larger exchangeable Mg and Na pools for the whole  
245 soil profile (to 30 cm depth) than birch, with pine intermediate (Table 5). Spruce stands also  
246 tended to have the largest  $\text{CEC}_{\text{eff}}$  and amounts of exchangeable Ca and K, although these  
247 differences were not significant (Table 5). In the humus layer, spruce stands had significantly  
248 larger exchangeable K, Ca, Mg and Na pools than pine and birch stands (Figure 4). The  
249 exchangeable base cation pool in the soil was larger in spruce stands compared with birch  
250 ( $P=0.054$ ). Pine stands tended to have larger exchangeable K, Ca, Mg and Na pools than birch  
251 in the humus layer, although the difference was only significant for Ca (Figure 4b) and Mg  
252 (Figure 4c). In spruce and pine stands, the base cation pool decreased with depth, except for  
253 Na, which increased with depth in pine stands and showed no significant differences with  
254 depth in spruce stands (Figure 4d). In birch stands, differences with depth were small and not  
255 significant, except for Na, which increased with depth. Base saturation in the humus layer was  
256 significantly higher in birch (79%) than in spruce stands (52%), with pine intermediate (70%),  
257 whereas there were no significant differences between species in the mineral soil (Figure 5).  
258 Aluminium content ( $\text{mol}_c \text{ m}^{-2}$ ) did not differ significantly between the species (Table 5).  
259 However, for all species there were significantly smaller amounts of Al in the humus layer  
260 ( $0.002\text{-}0.08 \text{ mol}_c \text{ m}^{-2}$ ) compared with the upper part of the mineral soil ( $0.6\text{-}0.8 \text{ mol}_c \text{ m}^{-2}$ ).

261

## 262 **4. Discussion**

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

### 272 *4.1 C, N and organic matter*

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

281           The higher production rate in the spruce stands, manifested as differences in basal area  
282 (Table 2), was not directly reflected in litter production (Figure 1), as pine and spruce stands  
283 did not differ in litter production, even though pine tended to have lower basal area than  
284 spruce (Table 4). One explanation for this is differences in needle longevity, as pine needle  
285 longevity is usually around 2 years, compared with 6 years for spruce needles (Reich *et al.*,  
286 1996), leading to the same needle litter production in pine and spruce stands even though  
287 spruce stands had larger canopies. Another explanation is the different amount of understorey  
288 vegetation. Understorey trees, which were not included in the overstorey tree basal area  
289 (Table 2), contributed to litter production in the pine and birch stands, but were absent in the  
290 spruce stands. Differences in C and N content may also be explained by differences in below-  
291 ground production. Kleja *et al.* (2008) showed that root litter production in spruce forests can  
292 be of the same magnitude as above-ground litter production.

293 A higher decomposition rate of birch foliage compared to Scots pine and Norway  
294 spruce foliage (Mikola, 1960; Palviainen *et al.*, 2004) may have contributed to the difference  
295 in soil organic matter pools. Palviainen *et al.* (2004) reported larger mass losses in silver birch  
296 and Scots pine leaf and root litter compared with Norway spruce needle and root litter in  
297 Finland. They also found that differences between birch and pine were small after three years  
298 of decomposition. Slower decomposition of Norway spruce litter can be explained by higher  
299 lignin content, although lignin concentrations vary within species. According to Johansson  
300 (1995) lignin content of Norway spruce needles was 32 %, 26 % and 28 % in Norway spruce,  
301 Scots pine and silver birch foliage, respectively. Berg and Mentemeyer (2002) found higher  
302 lignin concentrations in conifer needles than in birch leaves, but Reich *et al.* (2005) found  
303 higher lignin contents in silver birch than in pine and spruce. Furthermore, decomposition in  
304 birch stands is often enhanced by the presence of earthworms, mixing the soil and increasing  
305 C and N mineralisation (Saetre, 1998).

306 The litter quality and mineralisation rate differ between deciduous and coniferous  
307 species (e.g. Krankina *et al.*, 1999; Polyakova and Billor, 2007; Menyailo, 2009) and also  
308 between pine and spruce (Stendahl *et al.*, 2010). Field layer vegetation can be an important  
309 contributor to the litter layer, sometimes making up half the total litter production (Stålfelt,  
310 1960). In the present study, the field and bottom layer in the birch and pine stands is  
311 dominated by grass, shrubs, ericoid plants and ferns, whereas the forest floor in the spruce  
312 stands is covered with mosses (Table 2), with a lower litter quality and decomposition rate  
313 (Turetsky *et al.*, 2010). This is consistent with the lack of field layer in 40% of spruce plots in  
314 southern Sweden reported by Stendahl *et al.* (2010). When including the contribution of the  
315 field layer vegetation to litter production, the litter fall in the birch stands may have been of  
316 the same magnitude as that in the spruce stands (Table 4).

317 The thicker humus layer observed in spruce stands in the present study (Table 3) is consistent  
318 with findings in other studies (e.g. Priha, 1999; Smolander *et al.*, 2005) and may explain  
319 observed differences in C stocks between species (Table 5). Our results are also in agreement  
320 with a soil survey of 30 forest sites in Finland (Liski and Westman, 1995) and an analysis of  
321 soil C data from the Swedish National Forest Soil Inventory (Stendahl *et al.*, 2010). However  
322 since they included stands with different background, they were unable to distinguish between  
323 differences in species composition and differences in soil parent material composition. In the  
324 present study, there were more obvious species differences in C pools in the humus layer than  
325 in the mineral soil. In spruce stands, the humus layer contained 44% of the total carbon stock  
326 down to 30 cm depth in mineral soil (3.2 kg C m<sup>-2</sup>), whereas the humus layer in the birch

327 stands only contained 15% of total carbon stock ( $0.6 \text{ kg C m}^{-2}$ ), with pine intermediate (34%,  
328  $1.7 \text{ kg C m}^{-2}$ ). These numbers are consistent with the  $2.8 \text{ kg C m}^{-2}$  in the humus layer (35% of  
329 total C stock to a depth of 50 cm) reported for Swedish podsoles by Olsson *et al.* (2009).

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

336 The different amounts of soil nitrogen in spruce and birch stands, amounting to  
337 approximately  $1000 \text{ kg N ha}^{-1}$ , corresponds to an annual net difference in soil nitrogen  
338 accumulation rate of  $20 \text{ kg ha}^{-1} \text{ year}^{-1}$  during a 50 year stand age. In addition, differences in  
339 basal area between, in particular, spruce and birch stands, suggest higher nitrogen  
340 accumulation in spruce biomass, which would add further to the discrepancy in total nitrogen  
341 pools between the birch and the spruce stands. Higher deposition of nitrogen in coniferous  
342 forests compared to deciduous may partly explain this difference. Nitrogen deposition is  
343 currently high,  $>10 \text{ kg ha}^{-1} \text{ year}^{-1}$  (Karlsson *et al.*, 2010) in south-west Sweden, where the  
344 study site is located. A Swedish study reports 1.5 to 3 times higher total deposition  
345 (throughfall + stemflow) of  $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$  and  $\text{SO}_4\text{-S}$  in spruce canopies compared with  
346 birch and beech canopies (Bergkvist and Folkesson, 1995). Coniferous stands – which are  
347 often taller than deciduous stands, with higher leaf area index and longer foliage longevity –  
348 usually intercept more nitrogen and sulphur as dry deposition than deciduous species  
349 (Augusto *et al.*, 2002; De Schrijver *et al.*, 2007). It is likely that differences in soil nitrogen  
350 storage were also caused by differences in decomposition and nitrogen turnover rates.  
351 Nitrification is linked to C:N ratio, with higher nitrification rate with lower C:N ratio (e.g.  
352 Andersson *et al.*, 2002; Ross *et al.* 2009) suggesting higher nitrification in the birch stands.  
353 Ross *et al.* (2009) also found a correlation to proportion of coniferous species, with less  
354 nitrification in conifer dominated stands than in broadleaf stands. An additional cause to the  
355 different nitrogen accumulation rates could therefore be a greater nitrate leaching from the  
356 birch stands compared to the coniferous stands. However, even with large differences in N  
357 deposition and leaching, part of the nitrogen is still unaccounted for and further studies are  
358 needed to explain this difference.

359 The low humus layer C:N ratio in birch stands compared with conifer stands (Figure 2c)  
360 was expected, as birch litter C:N ratio was also lower (Table 4). The C:N ratio is used to  
361 describe litter quality, and deciduous species often have a lower C:N ratio than pine and  
362 spruce (Mikola, 1985; Priha and Smolander, 1999; Smolander et al., 2005; Menyailo,  
363 2009). Similarly, North American studies have shown that an increased admixture of  
364 foliage litter from deciduous trees with coniferous litters decrease the overall C:N ratio  
365 of the litter (Sanborn, 2001; Polyakova and Billor, 2007).

#### 366 4.2 Soil acidity and mineral nutrients

367 Tree species can influence the acid-base status of soils in different ways. Firstly,  
368 qualitative differences in the acid-base status of soils between tree species may develop due to  
369 differences in litter quality (degradability) and base content of the litter, and differences in  
370 litter quality may also influence the composition of the decomposer communities. Secondly,  
371 quantitative differences can develop when a species with faster growth rate and faster nutrient  
372 accumulation rate accumulates more excess cations (compared with anion uptake) in biomass,  
373 leading to greater soil acidification (e.g. Nilsson *et al.*, 1982). Another quantitative effect may  
374 result from differences in canopy structure, in particular differences between deciduous and  
375 evergreen trees, due to different capacities to intercept dry deposition, e.g. acidifying  
376 ammonium and sulphate deposition, as well as base cations (De Schrijver *et al.*,  
377 2007). Thirdly, species, with dissimilar rooting patterns, may differ in uptake of nutrients from  
378 subsoils. Deeply rooted tree species are often assumed to pump cation nutrients from deeper  
379 soil horizons and depositing them in litter at soil surface. However, these effects are poorly  
380 estimated (Binkley, 1995).

381 In the present study, we found that pH in the humus layer and upper part of the  
382 mineral soil was higher in the birch stands than in the coniferous stands (Figure 3). In  
383 addition, base saturation followed the same pattern as pH, with significantly higher base  
384 saturation in birch stands than in spruce stands, with pine intermediate (Figure 5). These  
385 effects, which account for the qualitative differences in the acid-base status of the uppermost  
386 soil layers, are consistent with those reported in many other studies comparing the soil status  
387 of different stands. For example, the Swedish Survey of Forest Soils and Vegetation (Nilsson  
388 *et al.*, 2007) reported an average pH in the humus layer of 4.16, 3.75 and 3.87 for Swedish  
389 birch, pine and spruce stands, respectively. Several other studies have shown higher pH in  
390 humus layers of deciduous forests in pure stands or in admixtures compared with coniferous  
391 forests (e.g. Hallbäck and Tamm, 1986; Brandtberg *et al.*, 2000; Hagen-Thorn *et al.*, 2004;

392 Oostru et al., 2006), and . Differences in pH between pine and spruce stands are often small  
393 (e.g. Smolander and Kitunen, 2002) and even though pine stands often have a lower soil pH  
394 than spruce stands (e.g. Reich *et al.*, 2005; Nilsson *et al.*, 2007), the opposite, as in our study,  
395 has also been reported (e.g. Priha and Smolander, 1999). Other studies have also shown that  
396 stands of deciduous species often have a higher base saturation than conifer stands (e.g. Reich  
397 *et al.*, 2005; Nilsson *et al.*, 2007). The relatively high base saturation in the pine stands in the  
398 present study may have been an effect of the greater abundance of deciduous trees, shrubs and  
399 grasses in the understorey vegetation (Table 2).

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

405 Differences in canopy structure also have the potential to influence soil pH. Bergkvist  
406 and Folkesson (1995) reported 2 to 8 times higher dry-deposited acidity ( $H^+$ ) in spruce  
407 canopies than in deciduous. Even though most of the acidity is neutralised by the foliage, dry-  
408 deposited acidity can explain part of the difference in soil pH between species. Nilsson *et al.*  
409 (2007) suggest that a larger deposition of acid substances in spruce stands in south-west  
410 Sweden evens out the pH differences in humus layers under pine and spruce stands in the  
411 region.

412 Our prediction that the exchangeable base cation pools in the soil would be  
413 ranked in the order birch > pine > spruce, due to expected greater tree biomass and nutrient  
414 accumulation in the spruce stand, was not supported by the results. Instead, the reverse  
415 ranking between species was observed for the base cations, with lower exchangeable cation  
416 pools (Table 5) in the birch stands than in the spruce stands. We can only speculate about the  
417 causes for these results. Lower dry deposition of base cations in birch forests could partly  
418 account for the smaller soil base cation pools (Bergkvist and Folkesson, 1995). However, the  
419 possibility cannot be excluded that more rapid weathering rates and lower leaching losses in  
420 the spruce stands compared with the birch stands have contributed to the different  
421 exchangeable base cation pools. Higher leaching of base cations may have occurred in  
422 companion with potentially higher nitrate leaching in birch stands. The coniferous stands had  
423 a higher content of soil organic matter and higher cation exchange capacity, suggesting a  
424 higher flux of base cations to the soil through litter fall, as well as a higher retention capacity  
425 due to the higher cation exchange capacity. Our results indicate that choice of tree species



426 may have an impact on soil base cation pools in the same order of magnitude as the impact of  
427 harvesting intensity. Akselson *et al.* (2007) showed that whole-tree harvesting, which is  
428 increasing in Sweden due to growing interest in biofuels, reduces nutrient pools compared to  
429 stem-harvesting.

430 The exchangeable pools of cations in the present study were of similar magnitude to  
431 other observations of cation pools at Norway spruce sites in the Tönnersjöheden forest  
432 (Olsson *et al.*, 1996). Furthermore, the forest soils of glacial origin in this region tend to  
433 have low exchangeable Ca pools compared with those in other parts of Sweden (Anonymous,  
434 2010b). In this respect, the lower exchangeable pool of base cations in birch stands compared  
435 with spruce stands ( $P=0.054$ ) indicates a lower acid neutralising capacity (ANC) in birch  
436 compared with spruce stands. In conclusion, our results indicate that birch stands, compared  
437 with spruce stands in particular, produce less acid soil organic matter but also result in lower  
438 ANC and available pools of base cation nutrients.

#### 439 *4.3 Conclusions*

440 Our results show that less than one rotation period is enough for clear  
441 differences to emerge in many soil properties, particularly in the humus layer, between birch,  
442 pine and spruce stands growing on similar soils. Some of our hypotheses were confirmed,  
443 with higher soil pH and base saturation and thinner humus layers in birch stands and less  
444 carbon and nitrogen stored in the soil compared with pine and spruce stands. However, our  
445 prediction of a larger pool of exchangeable base cations in birch stands was rejected, since  
446 soil exchangeable base cation storage tended to be larger in spruce stands than birch, despite  
447 larger basal area in the spruce stands. Our study separates the effect of tree species on soil  
448 properties from confounding effects such as soil texture, geochemistry and climate. Our  
449 results are in agreement with previous findings on correlations between dominant species and  
450 soil properties. Spruce forests seem to sequester more soil carbon than pine and birch forests;  
451 however, this is connected with a lower soil pH and base saturation.

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## 596 Tables

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

598

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

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600

601 Table 2. Basal area ( $\text{m}^2 \text{ha}^{-1}$ ) of overstorey trees, measured at 130 cm (diameter breast height, DBH); and of  
 602 shrub layer in birch and pine stands, measured at root collar (diameter at base, DAB) and, when applicable, at  
 603 130 cm (many shrubs were shorter than 130 cm, with no measured DBH); bottom and field layer biomass (g dw  
 604  $\text{m}^{-2}$ ), sorted into grasses, forbs, ericoids, mosses and trees (<50 cm height) (n=3 spruce, pine, n=2 birch, least  
 605 squares means  $\pm$  SE). Different letters indicate significant differences between species ( $P < 0.05$ ), n.s. = not  
 606 significant  
 607

		<i>Silver birch</i>		<i>Scots pine</i>		<i>Norway spruce</i>	
<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 $\text{m}^{-2}$ )	157 $\pm$ 11	a	119 $\pm$ 35	a	0 $\pm$ 0	b
Forbs	(g dw $\text{m}^{-2}$ )	25 $\pm$ 6	n.s.	22 $\pm$ 8		0 $\pm$ 0	
Ericoids	(g dw $\text{m}^{-2}$ )	17 $\pm$ 15	n.s.	69 $\pm$ 27		0 $\pm$ 0	
Mosses	(g dw $\text{m}^{-2}$ )	69 $\pm$ 12	ab	38 $\pm$ 3	a	237 $\pm$ 61	b
Trees	(g dw $\text{m}^{-2}$ )	10 $\pm$ 5	n.s.	15 $\pm$ 11		0 $\pm$ 0	
Total	(g dw $\text{m}^{-2}$ )	285 $\pm$ 9	n.s.	263 $\pm$ 19		237 $\pm$ 61	

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611 Table 3. Depth of humus layer; stone and boulder percentage to 30 cm depth; sand and clay content at 30 and 70  
612 cm depth and soil geochemistry at 70 cm depth (n=3 spruce, pine, n=2 birch, least squares means± SE). Different  
613 letters indicate significant differences between species (P<0.05), n.s. = not significant

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

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617 Table 4. Amounts of elements in litterfall (n=3 spruce, pine, n=2 birch, least squares means  $\pm$  SE). Different  
 618 letters indicate significant differences between species ( $P < 0.05$ ), n.s. = not significant

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

619

620

621 Table 5. Amounts of C and N, and exchangeable Ca, K, Mg, Na, Al, sum of exchangeable base cations (EBC),  
 622 effective cation exchange capacity ( $CEC_{eff}$ ) exchangeable acidity (EA) and C:N ratio in soil, including humus  
 623 layer and mineral soil 0- 30 cm (n=3 spruce, pine, n=2 birch; least squares means  $\pm$  SE). Different letters  
 624 indicate significant differences between species ( $P < 0.05$ ), ns = not significant  
 625

		<i>Silver birch</i>		<i>Scots pine</i>		<i>Norway spruce</i>	
C	(Mg ha <sup>-1</sup> )	40.8 $\pm$ 11.2	a	49.2 $\pm$ 7.5	a	72.7 $\pm$ 9.9	b
N	(Mg ha <sup>-1</sup> )	2.40 $\pm$ 0.70	a	2.69 $\pm$ 0.41	ab	3.49 $\pm$ 0.42	b
Ca	(kg ha <sup>-1</sup> )	62.0 $\pm$ 13.8	ns	79.1 $\pm$ 12.3		94.4 $\pm$ 14.7	
K	(kg ha <sup>-1</sup> )	53.7 $\pm$ 11.3	ns	51.3 $\pm$ 5.6		65.6 $\pm$ 3.8	
Mg	(kg ha <sup>-1</sup> )	18.1 $\pm$ 4.1	a	25.3 $\pm$ 3.8	a	39.6 $\pm$ 4.5	b
Na	(kg ha <sup>-1</sup> )	33.6 $\pm$ 7.0	a	35.8 $\pm$ 3.8	a	49.7 $\pm$ 6.6	b
Al	(kmol <sub>c</sub> ha <sup>-1</sup> )	13.5 $\pm$ 5.1	ns	14.0 $\pm$ 2.6		19.7 $\pm$ 4.6	
EBC	(kmol <sub>c</sub> ha <sup>-1</sup> )	7.75 $\pm$ 1.62	ns	8.90 $\pm$ 1.22		11.8 $\pm$ 1.4	
$CEC_{eff}$	(kmol <sub>c</sub> ha <sup>-1</sup> )	45.6 $\pm$ 13.6	ns	45.9 $\pm$ 5.5		64.4 $\pm$ 7.9	
EA	(kmol <sub>c</sub> ha <sup>-1</sup> )	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

626

627

628 **Figure captions**

629 **Figure 1.** Relationship between fine litterfall and overstorey basal area of stands. S=spruce,  
630 P=pine, B=birch, 1-3 = different blocks.

631

632 **Figure 2.** Differences in a) amount of carbon ( $\text{g m}^{-2}$ ), b) amount of nitrogen ( $\text{g m}^{-2}$ ), and c)  
633 C:N ratio at different soil depths (n=3 spruce, pine, n=2 birch; least squares means  $\pm$  SE).

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

636

637 **Figure 3.** Differences in pH ( $\text{H}_2\text{O}$ ) at different soil depths (n=3 spruce, pine, n=2 birch; least  
638 squares means). Different letters indicate significant differences between species ( $P<0.05$ ), ns  
639 = not significant.

640

641 **Figure 4.** Differences in amount of base cations for a) potassium, b) calcium, c) magnesium,  
642 and d) sodium at different soil depths (n=3 spruce, pine, n=2 birch; least squares means  $\pm$  SE).

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

645

646 **Figure 5.** Differences in base saturation (%) at different soil depths (n=3 spruce, pine, n=2  
647 birch; least squares means  $\pm$  SE). Different letters indicate significant differences between

648 species ( $P<0.05$ ), ns = not significant.

649

Figure 1.

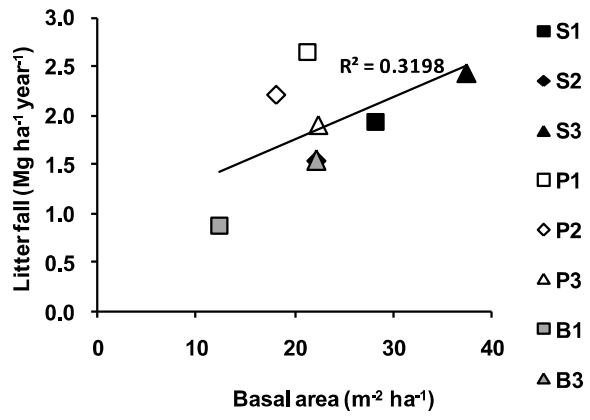
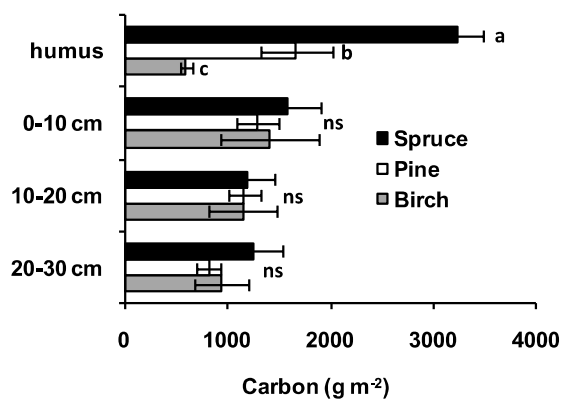
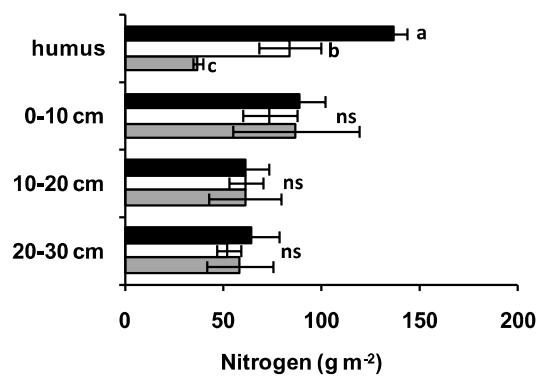


Figure 2.

a)



b)



c)

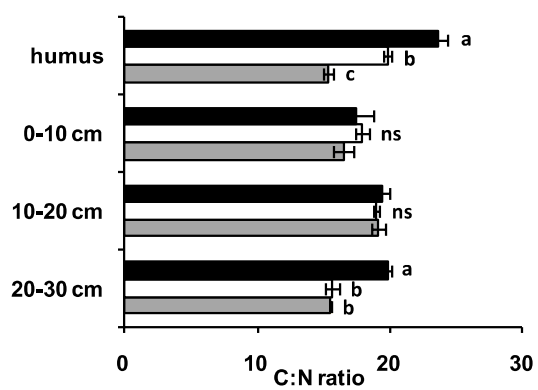


Figure 3.

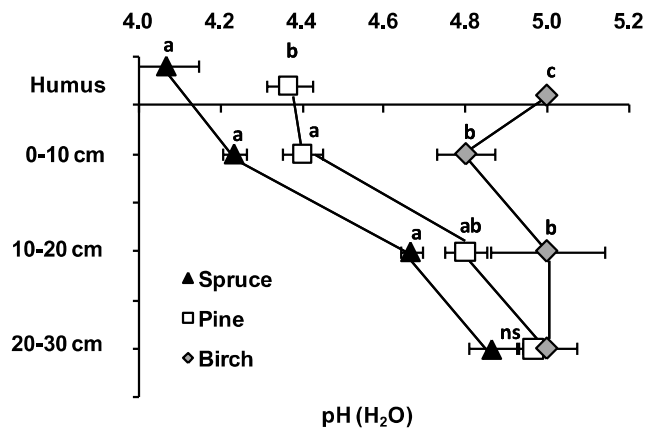
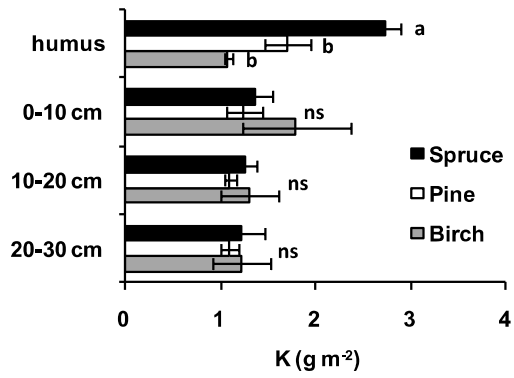
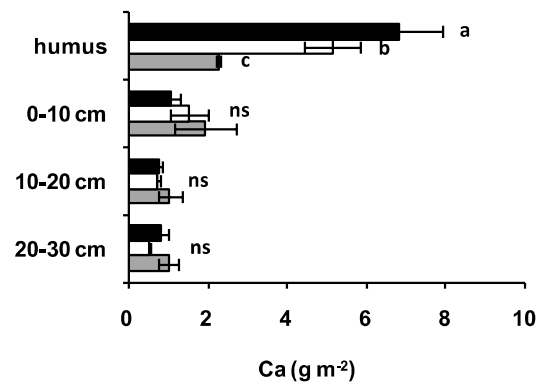


Figure 4.

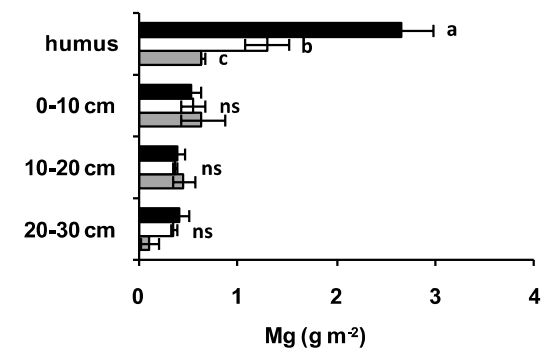
a)



b)



c)



d)

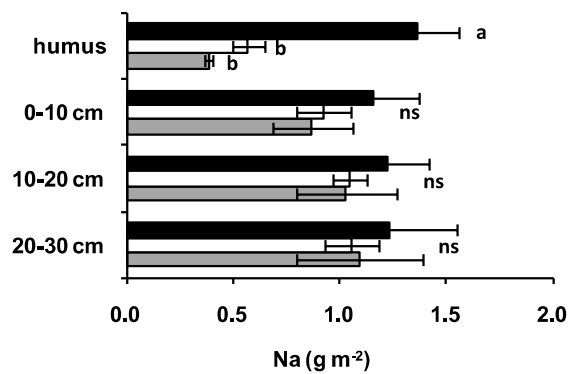




Figure 5

