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Soil Organic Carbon in Swedish Spruce and Pine Forests – Differences in Stock Levels and Regional Patterns

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The selection of tree species is one factor to consider if we want to mitigate carbon dioxide emissions to the atmosphere through forest management. The objectives of this study were to estimate the differences in soil organic carbon (SOC) stocks under Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) forests and to examine causes of differences in the accumulation of carbon in the forest soil. Large-scale inventory data was used to quantify variations in SOC stock in relation to stand type and the accumulation of carbon for spruce and pine stands was analysed by simulation. Based on field data, the national mean SOC stock was 9.2 kg m^{-2} in spruce dominated stands and 5.7 kg m^{-2} in pine dominated stands. For both species, the SOC stock, measured in the field inventory, increased significantly with increasing temperature, although at different rates. The SOC stock was larger for spruce under all temperature conditions, but the difference between species diminished with increasing temperature. The simulations indicated that the build-up of SOC over several rotations was 22% higher in spruce stands than in pine stands under similar environmental conditions. The main difference was found to be the greater input of harvest residues for spruce. Further, the simulations showed that ground vegetation contributed considerably more to the litter production under pine than under spruce. On sites where both Scots pine and Norway spruce are considered suitable, the latter should be selected if the aim of the forest management policy is to maximize the accumulation of SOC in the forest. Further, spruce is more favourable for SOC accumulation in areas with cold temperatures and on sites with low productivity.

Keywords forest management, Norway spruce, Scots pine, soil carbon, temperature sum, tree species, simulation
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1 Introduction

Forest management strategies may have great potential to mitigate carbon dioxide emissions to the atmosphere (Johnson 1992, De Wit and Kvindesland 1999, Eriksson 2007) and the selection of tree species could be an important factor in such strategies. One important aspect of mitigating carbon dioxide emissions is the extent to which organic carbon is accumulated in the soil. Under boreal conditions in Scandinavia the main choice for a forester is often between Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), where site conditions are suitable for the two species. However, it is not clear which tree species provides the best option for maximising carbon accumulation in the soil.

In Swedish studies reviewed by Gärdenäs (1998), Norway spruce (*Picea abies* (L.) Karst.) stands contained a significantly higher amount of soil organic matter in the forest floor (combined L-, F- and H-layers) than stands of silver birch (*Betula pendula* Roth) and Scots pine (*Pinus sylvestris* L.). In European studies, pine forests often have remarkably low soil carbon pools (Jandl et al. 2007), even though pine is often found on shallow and dry soils. In contrast, Norwegian studies have found lower levels of accumulated carbon under Norway spruce stands than Scots pine stands, but more than under birch stands (De Wit and Kvindesland 1999).

Johnson (1992) stated that the effect of tree species on soil organic carbon (SOC) is often significant but inconsistent. The effect of tree species on carbon accumulation in the soil can be attributed to differences in biomass production, since higher production results in higher above- and below-ground litter production (Albrektsson 1988, Berg et al. 1999a, b). The total litter production depends on the relative biomass of different tree parts and their turnover rate, both of which vary among species. For example, spruce stands generally have a greater needle biomass than pine stands of the same age on soils with the same site conditions, but the turnover rate of pine needles is greater than that of spruce needles (Ågren and Hyvönen 2003).

Litter from different tree species decomposes at different rates (Olson 1963, Melillo et al. 1982, 1989, Prescott et al. 1993, Stump and Binkley 1993), thereby influencing soil carbon accumulation rates (McClaugherty et al. 1985). The decomposition rate is influenced by a number of interacting biotic and abiotic factors that are more or less affected by the tree species, for example litter quality, the composition of the decomposer community, microclimate and pH (Fogel and Cromack 1977, McClaugherty et al. 1985, Kirschbaum 1995). Properties that reflect litter quality include: nutrient content, C:N ratio, lignin content (acid resistant fraction), and lignin:N ratio (Staaf and Berg 1982, Melillo et al. 1982, Gower and Son 1992, Prescott et al. 1992, Stump and Binkley 1993), which all vary with tree species. For example, it has been found that needle litter of Norway spruce has significantly higher concentration of nutrients and resistant organic C than that from pine, when growing under similar site conditions (Johansson 1995). The nutritional status of litter does not depend only on species, but also to some degree on soil fertility (Fernandez and Struchtemeyer 1984, Miller 1984, Liu and Trüby 1989). This suggests that it is difficult to separate site-specific influences from tree-specific differences in the accumulation of SOC.

Ground vegetation (field and bottom layers) contributes to the litter on the forest floor, and the impact of this contribution depends on available light and nutrient conditions. A negative correlation has been found between the canopy cover of trees and the development of the field layer (Persson and Hytteborn 1975). Productive Norway spruce stands tend to be dense and litter from the field layer is therefore expected to contribute less to the total litter as a result of intense shading. This is not the case for Scots pine stands, where dwarf shrubs can make a substantial contribution to the total litter. This was evident in a study by Persson (1980), who found equal contributions of dwarf shrub litter and needle litter in a young Scots pine stand in central Sweden. In southern Finland, ground vegetation has been found to account for half the total above-ground litter in Scots pine stands (Mälkönen 1974).

The methodological approaches for studying the effects of different tree species on soil carbon include controlled experiments, although few studies are available. In addition, survey data may provide information about variations in soil carbon stock and the effect of forest type (Grigal and Ohmann 1992, Liski and Westman 1997). This approach provides robust results although interpretation may be difficult due to confounding effects, for example the covariance between tree species and site conditions. Mechanistic models can be used to integrate knowledge about different processes in order to estimate the effect of tree species on the SOC stock and provide insights into the mechanisms contributing to the differences. For example, Ågren and Knecht (2001) simulated the soil carbon accumulation associated with Scots pine and Lodgepole pine (*Pinus contorta*) stands that varied in their productivity and litter quality. Differences in SOC stock for Norway spruce and Scots pine have been simulated by Ågren and Hyvönen (2003) and Peltoniemi et al. (2004).

The objectives of this study were 1) to quantify differences in SOC stock between Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) forests with similar site conditions, 2) to investigate differences in litter production, and 3) how different litter types contribute to the C accumulation. This may help to identify suitable tree species for promoting soil carbon storage in boreal forests. Two approaches were used to investigate the soil carbon in stands of Scots pine and Norway spruce. Field data was used to quantify the SOC stock in managed stands of spruce and pine, while empirical forest growth models and a mechanistic decomposition model were used to study the impact of annual litter fall and input of harvest residues on the build-up detrital and soil C stock in a pine and a spruce stand, respectively.

2 Materials and Methods

2.1 Field Data

The field data in this study were taken from the Swedish National Forest Soil Inventory (NFSI), which is carried out using the permanent plots of the National Forest Inventory (Ranneby et al. 1987). The NFSI covers all of Sweden except for arable land, urban areas and the mountain ranges, and encompasses ca 23 500 permanent plots, each with a radius of 10 m. These are revisited every 10 years. The plots represent a stratified random sample of Swedish forest soils. Soil sampling and analyses are carried out in a sub-sample of the plots. For this study, data from the period 1993–2002 were used.

The data analysed in the present study were limited to plots containing only Scots pine or Norway spruce trees (i.e. 100% of basal area of one of the species) and with a mean basal area weighted diameter > 10 cm. Furthermore, the data was limited to Podzol soil types with a dominant soil texture class not coarser than sand, and a mesic to mesic/moist soil moisture class. These criteria were used in order to select plots fulfilling the site demands for both tree species. In total, 332 plots were included in the analysis.

Soil sampling was made according to three diagnostic horizons (O-, B- and C-), and from one fixed depth (BC sample). The entire depth of the O-horizon (excluding the litter (L) layer) was sampled using a core sampler with a diameter of 10 cm at 1 to 9 points around the plot centre until ca 1 kg fresh humus material was collected. The B-horizon was sampled from the upper 5 cm, the BC sample was sampled at 45–50 cm depth from the ground surface, and the C-horizon was sampled at 55–65 cm from the top of the mineral soil, i.e. at variable depth from the ground surface depending on the thickness of the O-horizon. No sampling was made in the E(A)-horizon. The samples were homogenised, sieved and dried to constant weight at 35 °C; living and dead roots > 1 mm were removed. The total organic carbon content of soil material < 2 mm was analysed using an elemental analyser (LECO CNS-1000). The pH was determined in water, while exchangeable cations (Na, K, Ca and Mg) were extracted with 1 M ammonium acetate at pH 7.00 and analysed by plasma-emission spectrometry (ICP-ES). Total acidity was determined in the same extract by titration with 0.1 M NaOH.

The site factors for the plots used in this study are presented in Table 1. Temperature sum was defined as the sum of daily mean temperature exceeding +5 °C and calculated with a function based on latitude and altitude (Odin et al. 1983). Site quality was defined as the capability of a site to produce wood, i.e. the mean production of stem wood (m^3 ha^{-1} yr^{-1}) from stump to the top of the tree (including bark) over one rotation (Hägglund

Table 1. Descriptive statistics for the site factors for spruce (n = 144) and pine inventory plots (n = 188).

	Spruce		Pine	
	Mean	(S.E.)	Mean	(S.E.)
Temperature sum (degree days)	1042	(26.1)	898	(13.7)
Latitude	60.9	(0.27)	63.8	(0.2)
Elevation (m a.s.l.)	304	(13.6)	300	(9.59)
Site quality (m^3 ha^{-1} yr^{-1})	6.81	(0.28)	3.89	(0.11)
Tree height (m)	18.5	(0.46)	14.5	(0.31)
Stand age (years)	89.4	(3.84)	85.3	(3.05)
pH in O-horizon	3.9	(0.03)	3.71	(0.02)
pH in C-horizon	5.13	(0.03)	5.23	(0.02)
CEC [a] in O-horizon (mmol kg^{-1})	817	(21.4)	776	(17.2)
CEC [a] in C-horizon (mmol kg^{-1})	39.7	(2.41)	22.4	(1.65)
Base saturation in O-horizon (%)	20.0	(0.97)	15.3	(0.43)
Base saturation in C-horizon (%)	13.5	(1.7)	11.6	(0.9)

[a] CEC = Cation Exchange Capacity

and Lundmark 1981) and was retrieved from the National Forest Inventory. The field layer vegetation was classified for each site as follows: bilberry types, other dwarf shrub types, grass types, soil without field layer and herbs without dwarf shrubs (Hägglund and Lundmark 1981).

2.2 Calculation of Soil Carbon Stock

The calculation of the SOC stock in the O-horizon (kg m^{-2}) was based on the amount of sampled dry organic matter from the entire horizon depth (kg), the C concentration of the material analyzed (% of dry weight), and the soil core area multiplied by the number of cores sampled (m^2). The SOC stock in the mineral soil was calculated for each sampled layer using the following equation:

$$SOC_{mineral} = (C_{conc} / 100) * BD * d * (100 - V_{CF}) / 100 \qquad (1)$$

where $SOC_{mineral}$ is the amount of SOC in kg m^{-2}, C_{conc} is the carbon concentration as a % of dry weight (d.w.), BD is the bulk density in kg m^{-3}, d is the depth (m) of the layer, and V_{CF} is the volume (%) of coarse fragments > 2 cm. The bulk density for the mineral soil horizons was calculated from the carbon concentration using the equation by Nilsson and Lundin (2006):

$$BD = 1546.3 * EXP\left(-0.3130 * C_{conc}^{0.5}\right) \qquad (2)$$

where BD is the bulk density in kg m^{-3}, C_{conc} is the carbon concentration as a % of d.w. Field observations of the frequency and size of surface boulders present within each plot were used as an indicator of the volume of coarse fragments. The values were chosen based on a large-scale inventory of coarse fragments in Swedish forest soils (Stendahl et al. 2009) by the rod penetration method (Viro 1952). For plots with many boulders (> 667 boulders per hectare) and with large boulders (diameter > 0.61 m), the volume was set to 50%. Plots with a moderate number of surface boulders (< 667 boulders per hectare) were allocated a volume of 30%, and those without any surface boulders were allocated a volume of 0%. These values are similar in magnitude to those found by Stendahl et al. (2009) in Swedish forest soils. The carbon concentration in the E(A)-horizon was not analyzed in the NFSI between 1993 and 2002. Therefore, an empirical function was derived from NFSI data from the period 1983–1987:

$$\begin{aligned} C_{conc\ E} = 7.0448 &+ (0.1758 * C_{conc\ B}) \\ &- (0.9047 * pH(H_2O)_B) - (10.77 * d_E) \\ &+ (19.0 * d_E^2) \\ &(r^2 = 0.21,\ n = 949) \end{aligned} \qquad (3)$$

where $C_{\text{conc E}}$ is an estimate of carbon concentration in the E-horizon, $C_{\text{conc B}}$ is the carbon concentration in the B-horizon, $\text{pH}(\text{H}_2\text{O})_\text{B}$ is the pH (H_2O) in the B-horizon, and d_E is the depth (m) of the E-horizon. For intermediate soil layers, which were not sampled, the SOC stock was estimated using the mean carbon concentration of the neighbouring measured layer(s). The thickness of these intermediate layers could be determined from the available depth information. Finally, total SOC stock for the 0–100 cm soil layer was calculated as the sum of the SOC stocks for each layer:

$$\begin{aligned}\text{SOC}_{0\text{–}100} = {} & \text{SOC}_{\text{O-horizon}} + \text{SOC}_{\text{E-horizon}} \\ & + \text{SOC}_{\text{B}(0\text{–}5)} + \text{SOC}_{\text{B-BC}} \\ & + \text{SOC}_{\text{BC-C}} + \text{SOC}_{\text{C-100}}\end{aligned} \tag{4}$$

2.3 Statistical Analysis

Descriptive statistics for all site factors were calculated (Table 1). To determine the relationship between the site factors and the SOC stock, a correlation matrix was created. In order to analyze the relationship between SOC and the temperature sum further, separate functions (using the General Linear Model, GLM) for Norway spruce and Scots pine were estimated and an F-test was used to determine whether the slopes differed significantly. Based on the estimated temperature sum, the sample plots were classified into temperature sum regions according to the following intervals: ≤750, 751–950, 951–1150, 1151–1350, and >1350 degree days (dd) (Fig. 1). Mean SOC stock and site quality were calculated for each temperature sum region and tree species. Statistical analyses for the GLM and Duncan's test for group means were used. All statistical analyses were undertaken using SAS 9.1 for Windows (SAS Institute Inc. 2004).

2.4 Simulation of Carbon Accumulation in Spruce and Pine Stands

2.4.1 Model for Stand Development

To simulate the influence of annual litter fall and the input of harvest residues on the build-up of SOC stock under different tree species, forest management strategies were developed for a hypothetical forest stand located in central Sweden (60°N, 16°E). This stand was given an altitude of 100 m a.s.l., and was defined to grow on a glacial till characterised by groundwater at a level of 1–2 m, with a Podzol soil type. The precipitation is on average about 700 mm per year and the annual mean temperature 5 °C in this area, which corresponds to a temperature sum of 1300 degree days. The potential production for the hypothetical stand was 7.0 $\text{m}^3\ \text{ha}^{-1}\ \text{year}^{-1}$ for the spruce stand, and of 6.4 $\text{m}^3\ \text{ha}^{-1}\ \text{year}^{-1}$ for the pine stand. Two simulations were performed, one with pure Norway spruce and one with pure Scots pine: 2200 seedlings ha^{-1} were assumed to have been planted and one pre-commercial thinning conducted. In both cases the stand comprised an

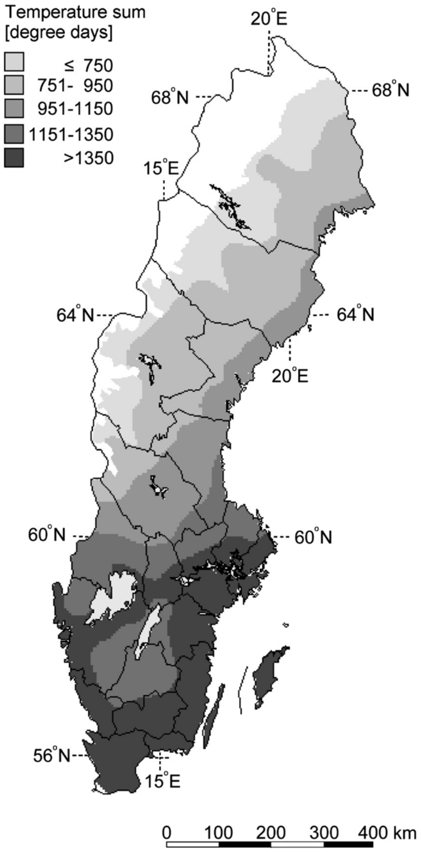

Fig. 1. Map of Sweden showing the distribution of different temperature sum regions.

even-aged monoculture.

Tree growth and thinning removals were simulated using a model combining two empirical growth models, one for the young forest up to a height of 10 m (Fahlvik and Nyström 2006), followed by another for growth leading to the formation of a mature forest (Ekö 1985). Both models are basically driven by site quality and stand density, affecting the height growth in the former and the diameter growth in the latter model; this results in robust model performance at the stand level. Due to limitations of the growth model for the young forest, the simulations were run from 16 years of age, with 1 760 trees ha^{-1} remaining from the plantation (80% survival rate) and an average tree height of 2.5 m and 3.0 m for Norway spruce and Scots pine, respectively. The transition between models was made by feeding the second model with the resulting basal area, stem density and age from the first model. The total (stem wood, branches, twigs and foliage) aboveground biomass of the trees was calculated using functions derived by Marklund (1988), while the biomass of the medium-sized roots (2–5 mm) and coarse roots (>5 mm) + stumps was calculated using biomass functions by Pettersson and Ståhl (2006). The tree biomass development from age zero to the age at 2.5 m height was assumed to increase linearly. Logging operations were modelled using recommendations by the Swedish Forest Agency (Swedish Forest Agency 1984), where the timing and intensity of thinnings and the timing of clear-cutting are based on the stand basal area and age. The thinning was evenly distributed among all tree sizes (i.e. the same percentage was removed according to both basal area and number of stems). Clear-cutting was set to occur when the basal area was near 39 m^{2} ha^{-1} for both species. This resulted in three thinning operations (at 37, 47 and 62 years of age for spruce and at 32, 47 and 62 years of age for pine), while clear-cutting occurred at 92 years for spruce and 97 years for pine. The time step in the second forest growth model was five years. The mean carbon stock in biomass during the simulation period was calculated as an indication of the significance of the standing biomass carbon stock, since the rotation length differed between the tree species. The carbon content of the biomass (dry weight) was assumed to be 50%.

2.4.2 Estimation of Litter Production

Annual litter production originates from different sources: branches, needles, medium-sized roots (2–5 mm), fine roots (<2 mm), and ground vegetation (field and bottom layer). The biomass of branches and needles was an output of the forest growth model (as described in the previous section). Annual litter input was calculated using biomass turnover rates for the different tree parts. For Norway spruce, the turnover rate for branches was set to 1.25% of the biomass (Muukkonen and Lehtonen 2004) and for needles to 11% of the biomass (Ågren et al. 2007). For Scots pine, the biomass turnover rate of branches was calculated using the function presented by Lehtonen et al. (2004) while the turnover rate for needles was set to 26% of the biomass (Ågren et al. 2007). The supply of fine root litter was set to 1.5 times the needle litter fall (Ågren et al. 2007) and the biomass turnover rate for medium-sized roots was assumed to be 10% for both species. Litter originating from harvest residues consisted of six biomass sources: branches, needles, stumps and coarse roots, medium-sized roots, fine roots, and the top of the stem. The biomass values were obtained from the forest growth models, with the exception of the stumps and coarse roots and the top of the stem, which were obtained using functions defined by Pettersson and Ståhl (2006) and yield tables produced by Laasasenaho (1975). The biomass of decayed fine roots from thinnings and clear-cutting was estimated as a proportion of needle biomass based on field data (Berggren Kleja et al. 2008). Litter production from the ground vegetation was estimated using biomass functions and biomass turnover rates presented by Peltoniemi et al. (2004).

2.4.3 Model for Litter Decomposition

The accumulation of carbon in the soil was modelled using the Q model (Ågren and Bosatta 1998), which is a mechanistic model for the decomposition of litter and soil organic matter (SOM) based on the continuous quality theory. SOM is comprised of a range of different carbon compounds of different qualities, which vary in their availability to decomposers. The model includes a parameter for the initial quality of different litter fractions. Annual input of fresh litter from different sources (i.e. needles, branches, stems, etc.) was tracked over time and the weight loss due to decomposition was calculated. The decomposition rate for the different litter fractions was controlled by the litter quality, the time it takes for decomposers to invade the litter, and factors describing the decomposing microbes. The model was formulated as follows:

$$
\begin{aligned}
G_{\mathrm{n}}(t) &= \frac{1}{\left(1+\alpha t\right)^{z}} \\
G_{\mathrm{w}}(t,t_{\max}) &= \frac{2}{\alpha(1-z)t_{\max}}\left[(1+\alpha t)^{1-z} - \left[1+\alpha(t-t')\right]^{1-z}\left(1-\frac{t'}{t_{\max}}\right)\right] \\
&\quad + \frac{2}{\alpha^{2}(1-z)(2-z)t_{\max}^{2}}\left\{\left[1+\alpha(t-t')\right]^{2-z} - \left[1+\alpha t\right]^{2-z}\right\} + \left(1-\frac{t'}{t_{\max}}\right)^{2} \qquad (5) \\
\alpha &= f_{C}\beta\eta_{11}u_{0}q_{0}{}^{\beta} \\
z &= \frac{1-e_{0}}{\beta\eta_{11}e_{0}} \\
t' &= \min(t,t_{\max})
\end{aligned}
$$

where $G_{\mathrm{n}}(t)$ is the remaining fraction of carbon from needle or fine root litter after time t and $G_{\mathrm{w}}(t,t_{\max})$ represents the remaining fraction from woody components. The parameter f_{C} (kg C $\mathrm{kg}^{-1}{}_{\text{dry mass}}$) is the C content of the decomposer biomass, β controls the change in decomposer growth rate with quality, η_{11} is the rate of decline in quality for each decomposition cycle, u_0 (yr^{-1}) is the decomposer growth rate, q_0 is the initial litter quality that depend on litter type, e_0 is the microbial efficiency, and $t_{\max}$ (yr) is the decomposer invasion time, i.e. when the coarse woody litter is totally invaded by microorganisms. Litter input data were transformed, by interpolation, into a time series of annual values, in order to comply with the one-year time step required by the Q model. Furthermore, the parameterization of the historic SOC stock was assumed to be the same for the simulated spruce and pine stands. The parameter values, given in Table 2, were set according to Ågren and Hyvönen (2003) with the exception of decomposer growth rate, u_0 (yr^{-1}), which was calculated based on a mean annual temperature of 5 °C (Ågren and Bosatta 1998). The decomposition data that was used for model parameterization were from Berg et al. (1991) for needle litter. For coarse woody litter it was based on a number of decomposition studies (Hyvönen et al. 2001). The same decomposition parameters were used for spruce and pine litter. Above-ground field and bottom layer vegetation litter was assumed to decompose in the manner of needles and below-ground litter in the manner of fine roots.

In order to better illustrate long-term differences, running average values for the combined detrital and SOC were calculated using a time-sequence equal to the rotation length. This dampened the large fluctuations associated with thinning operations and final fellings.

Table 2. Parameters used in the Q model for spruce and pine stands from Ågren and Hyvönen (2003), except for u_0 from Ågren and Bosatta (1998).

Parameter		Value
Decomposer C concentration (kg C $\mathrm{kg}^{-1}{}_{\text{dry mass}}$)	f_{C}	0.5
Decomposer growth rate (yr^{-1})	u_0	0.164
Microbial efficiency	e_0	0.25
Change in growth rate with quality	β	7
Decomposer invasion rate (yr)		
Branches	$t_{\max}$	13
Stems	$t_{\max}$	60
Initial quality of litter		
Needles	q_0	1.089
Fine roots	q_0	1.089
Woody litter	q_0	0.99
Quality decline through decomposition	η_{11}	0.36

2.4.4 *Validation of Simulated Litter Production*

To evaluate the estimates of the needle litter production in the present study, the simulation was compared with functions based on litter trap data. Functions developed for needle litterfall vs. basal area and latitude for Scots pine (Berg 1999b) and Norway spruce (Berg 1999a) were used. These functions are only applicable to mature forests and thus the simulated needle litter production for stands aged >37 yrs was compared with estimated litter production calculated from the empirical functions for the average basal area of the simulated stands, for the same age and for the same latitude (60°N).

3 Results

3.1 Field Data

The national average SOC stock from the field inventory plots was 9.2 kg m^{-2} (S.E. 0.3) for the spruce plots and 5.7 kg m^{-2} (S.E. 0.2) for the pine plots. This make up a 61% larger SOC stock for the spruce sites, while the average site quality was 75% higher for the spruce plots than for the pine plots (Table 1). The site factors that had the highest correlations to the SOC stock were latitude, temperature sum and site quality (Table 3). The linear relationships were all highly significant ($p<0.001$) and positive except for latitude, for which the relationship was negative. The other site factors included in the analysis also showed significant relationships, but with low values of the coefficient of determination ($R^2<0.2$).

The factor that corresponds most closely to the large scale climate gradient in Sweden is the temperature sum and this variable was investigated further to determine whether its relationship to the SOC stock was different for the two tree species. The temperature sum explained 32% of the variation in the SOC stock (Table 4), which increased significantly with increasing temperature sum (Fig. 2), although at different rates for the two species. As a consequence, the difference in SOC between the species was most pronounced at sites with low temperature sums (≤750 dd), where spruce plots contained on average ca. 4 kg more C m^{-2} than pine plots (Fig. 3B), whereas for sites with the highest temperature sums (>1450 dd), the difference was less than 1.5 kg m^{-2}. The SOC stock was significantly higher for spruce than for pine plots in those regions with temperature sum ≤1150 dd (Fig. 3B).

In the regions with temperature sums higher

Table 3. Correlation coefficients for linear relationships between different site factors and soil organic carbon stock in the 0–100 cm soil layer for spruce and pine inventory plots.

Factor	r	R^2	p
Latitude	–0.520	0.270	<0.001
Temperature sum	0.461	0.213	<0.001
Site quality	0.461	0.213	<0.001
CEC [a] in O-horizon	0.421	0.177	<0.001
pH in C-horizon	–0.350	0.123	<0.001
CEC [a] in C-horizon	0.304	0.092	<0.001
Elevation	–0.238	0.057	<0.001
Mean tree height	0.218	0.048	<0.001
Base saturation in C-horizon	–0.166	0.028	<0.01
Stand age	–0.160	0.026	<0.01
Base saturation in O-horizon	–0.129	0.017	<0.05
pH in O-horizon	–0.125	0.016	<0.05

[a] CEC = Cation Exchange Capacity

Table 4. Regression analysis between SOC in spruce and pine inventory plots and temperature sum (TSUM) (n = 144 for spruce and n = 188 for pine). The slopes for spruce and pine (P_{slope}) were compared to determine whether the lines were parallel.

Model: $Y_{ij}=a_i+b_iX_{ij}+\varepsilon_{ij}$	R^2	P_{model}	P_{slope}
$SOC_{spruce}=0.003(TSUM)+6.222$ $SOC_{pine}=0.007(TSUM)-0.165$	0.319	<0.001	<0.001

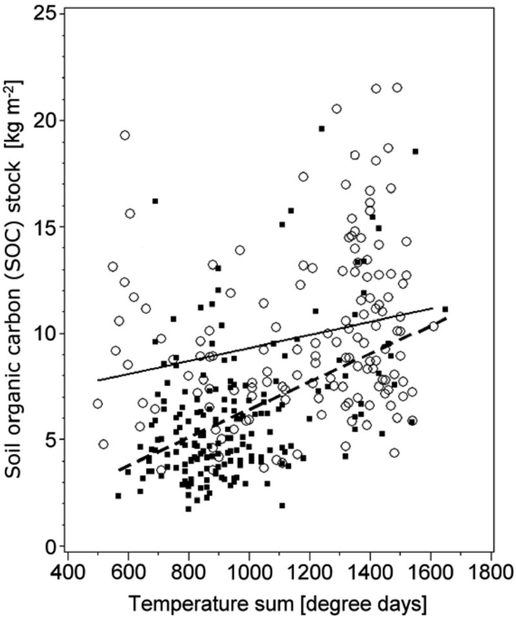

Fig. 2. Linear relationship between soil organic carbon (SOC) stock in the 0–100 cm soil layer and temperature sum for Scots pine plots (points: ■, fitted line: **---**) and Norway spruce plots (points: ○, fitted line: —). The difference in slope was significant ($R^2=0.319$, $p<0.001$, cf. Table 4).

than 750 dd, the site quality was significantly higher for spruce than for pine plots, with the difference increasing towards the south. There was, however, no significant difference in site quality in the coolest region (≤750 dd) (Fig. 3). The difference in site quality between the spruce and pine plots increased from 0.4 m^3 ha^{-1} yr^{-1} at temperature sums ≤750 dd to 4.4 m^3 ha^{-1} yr^{-1} for temperature sums >1350 dd.

The field layer vegetation cover, according to the field data, was substantially different between pine and spruce plots. As shown in Fig. 4, dwarf shrub types were dominant among both spruce and pine plots, in regions with a temperature sum less than or equal to 1150 dd. In the warmer regions, herb and grass types were more common among spruce plots, whereas the pine plots were dominated by dwarf shrub and grass types. Furthermore, in the warmest region (>1350 dd), the field layer was absent in as many as 40% of the spruce plots.

3.2 Simulation of Carbon Accumulation in Stands of Spruce and Pine

The model simulation showed that a Norway spruce stand may produce about 24% more biomass than a Scots pine stand during a single rotation period (92 years for spruce and 97 years for pine) when grown under identical site conditions: 0.51 and 0.41 kg d.w. m^{-2} yr^{-1} for spruce and pine, respectively. The mean carbon stock in

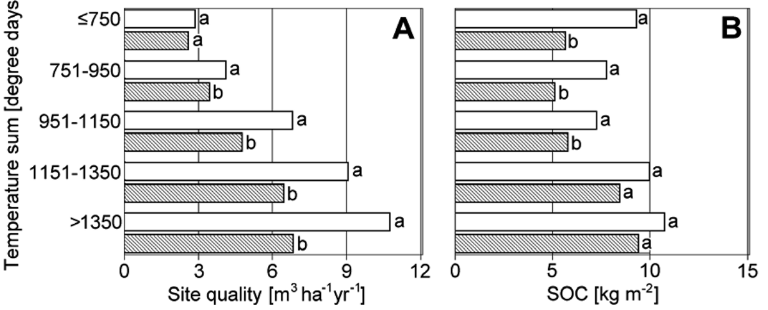

Fig. 3. Mean site quality (A) and soil organic carbon (SOC) stock in the 0–100 cm soil layer (B) in plots of pure Norway spruce (white bars) and Scots pine (grey bars) in different temperature sum regions in Sweden. Different letters indicate significant differences between plots with different tree species within each region ($p<0.05$).

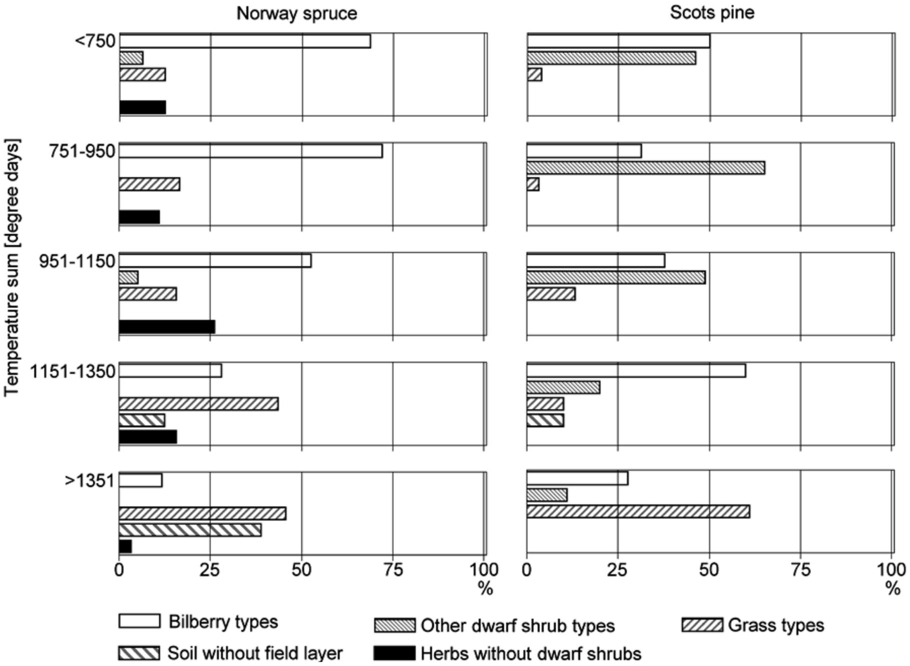

Fig. 4. Percentage occurrence of different field layer vegetation types for spruce and pine plots in different temperature sum regions in Sweden.

the above- and below-ground biomass was about 25% greater for spruce: 7.4 and 5.9 kg C m^{-2} for spruce and pine, respectively. In the simulation, the build-up of combined detrital and soil C stocks was larger for the spruce stand than the pine stand (Fig. 5). The difference between the two stands was about 41% (11.7 kg C m^{-2} for spruce and 8.3 kg C m^{-2} for pine) at the end of the first rotation, although this comparison largely reflects fresh litter and woody debris added with the clear felling, which was greater for spruce. A comparison of the running average stock values after three rotations resulted in a 22% larger value (5.7 kg C m^{-2} for spruce and 4.7 kg C m^{-2} for pine) for the detrital and soil C stock under the spruce stand than under the pine stand (Fig. 5). These running average values dampen the within rotation fluctuations and reflect the average long-term SOC accumulation for the forest stands.

According to the simulation, the spruce stand contained considerably more biomass than the pine stand, but the litter production rate for most biomass components were higher for pine. This resulted in just slightly larger contributions of

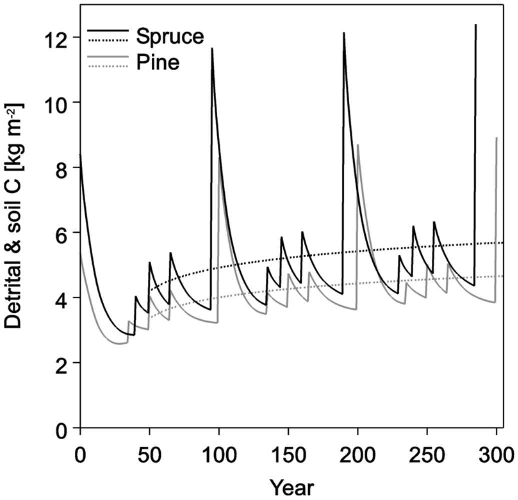

Fig. 5. Simulated amounts of newly accumulated detrital and soil C stocks (SOC) in pure spruce and pine forests (solid lines), respectively, during three rotations or ca. 300 years. Initial detrital and soil C stocks were assumed to be 0. Running average values (broken lines) were calculated using a time-sequence equal to the rotation length.

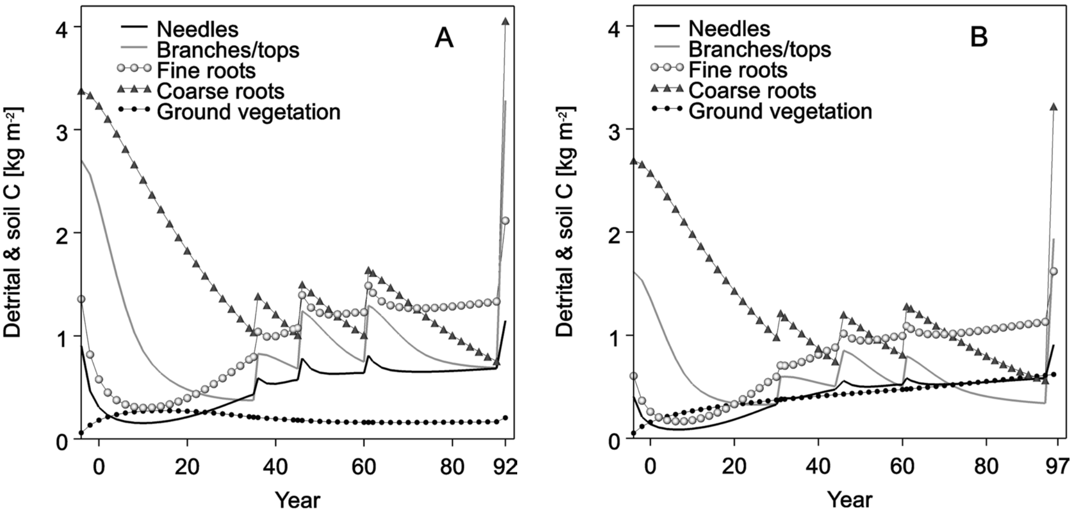

Fig. 6. Simulated amounts of detrital and soil C stocks derived from each biomass component in a spruce (A) and a pine (B) stand during the first rotation.

litter from needles, branches and fine roots to the build-up of the combined detrital and soil C stocks for spruce than for pine stands (Fig. 6A–B). For the spruce stand, however, there was a higher input of harvest residues as a result of the larger standing biomass, which resulted in more harvest residues (i.e. needles, branches and tops) remaining in the spruce stand. The litter from the ground vegetation contributed more to the build-up of the combined detrital and soil C stocks in the pine stand than the spruce stand, and its relative input for the pine stand was similar to that of needle litter (Fig. 6B). Furthermore, the annual litter input from the ground vegetation increased in the pine stand throughout the whole rotation, whereas in the spruce stand the contribution of ground vegetation decreased from about 20 years onwards. For both tree species, fine roots contributed most to the accumulation of the combined detrital and soil C stocks followed by needles, although coarse woody litter (coarse roots, branches and tops) also made a significant contribution (Fig. 6A–B).

Pine needle litter production was 0.18 kg C m^{-2} $year^{-1}$ when estimated with empirical functions based on litter traps and 0.16 kg C m^{-2} $year^{-1}$ based on our simulation, which was based on estimated needle biomass and its turnover rate. The corresponding figures for the spruce needle litter production were 0.17 and 0.18 kg C m^{-2} $year^{-1}$, respectively. These estimates indicate a generally good agreement despite the different approaches used.

4 Discussion

Many studies of Scots pine include sites with very poor conditions (Jandl et al. 2007), which may explain the low SOC levels reported for these forests. In the present study, we only included field sites on Podzol soil types with a dominant soil texture class no coarser than sand, with mesic to mesic/moist soil moisture class and similar site conditions (Table 1); i.e. all sites were suitable for both spruce and pine. Thus, typical pine sites of very low quality and very productive spruce sites, for example on Cambisols, were eliminated from the dataset. Despite this, a larger SOC stock was found under the spruce stands than the pine stands. To some degree, the large difference in national mean SOC stocks was influenced by differences in geographical distribution of the two species; spruce is more common towards the south and pine is more common towards the north of Sweden (Table 1). However, the higher SOC values for the spruce stands remained when grouping the data according to temperature sum regions.

The observed increase in SOC stock with increasing temperature sum and decreasing latitude (Table 3) is in accordance with previous reports describing the relationship between SOC stock and temperature gradients in the Fennoscandian boreal forest (Callesen et al. 2003, Liski and Westman 1997). Available solar energy and temperature have been shown to be the best predictors of the magnitude of coniferous litter fall at the European scale (Berg and Meentemeyer 2001). Furthermore, the temperature sum reflects the length of the active period for the processes involved in the SOC stock development, most importantly the net primary production and decomposition, as noted by Liski and Westman (1997). The increase in the SOC stock towards the south of Sweden may be the result of greater litter fall due to increasing productivity (Albrektsson 1988, Berg et al. 1999a, b) and/or a reduction in the decomposition rate due to a larger N deposition load (Martikainen et al. 1989, Nohrstedt et al. 1989). Nitrogen levels in fresh pine needle litter have been reported to range from about 3 mg g^{-1} in the north of Sweden to about 7 mg g^{-1} in the south (Berg et al. 1995). Litter with high N concentrations may ultimately not decompose as far and several mechanisms have been suggested to explain the phenomena. One is that the formation of new and stable complexes through incorporation of ammonium or nitrate into the humic complexes increases the recalcitrance of the residual organic matter (Stevenson 1994, Nömmik and Vahtras 1982). Another potential effect is suppression of the formation of lignolytic enzymes in lignin-degrading organisms in response to N deposition (Keyser et al. 1978, Kirk 1980). Consequently, any effect of temperature may be confounded by N-deposition or soil fertility gradients, both influencing net primary production and decomposition.

The relationships between inventory SOC and temperature sum exhibited different slopes for the spruce and pine stands (Fig. 2), indicating different responses in the plant–soil system. Liski and Westman (1997) also used a gradient approach for investigating the association between the SOC stock and temperature in Finland for *Calluna*-type (Scots pine dominated) and *Myrtillus*-type (Norway spruce dominated) forests. They found that SOC increased with temperature sum although, in contrast to our study, the rate of the increase was similar for the two forest types.

Although the current study was limited to sites that were suitable for both spruce and pine, the site quality was higher for the spruce stands than the pine stands across the whole of Sweden, with the exception of the coolest temperature sum region (≤750 dd) (Fig. 3). Further, there was an increasing difference towards the south. However, comparing the SOC stock under the two species with the site quality in different temperature regions, it was evident that site quality alone could not explain the differences (Fig. 3). For the coolest temperature region (≤ 750 dd), the mean site quality of the spruce and pine plots did not differ significantly, whereas the mean SOC stock in the spruce plots greatly exceeded that in the pine plots. Furthermore, in the two warmest temperature regions (>1150 dd), the spruce plots did not have a significantly larger SOC stock than the pine plots, despite the higher mean site quality.

Another factor that may contribute to the differences in SOC stocks is the type of ground vegetation, which differs substantially under the two tree species (Muukkonen and Mäkipää 2006). Further, its contribution to total litter fall varies between temperature sum regions and sites of different quality. The ground vegetation biomass is strongly correlated to the ground vegetation type and cover (Muukkonen et al. 2006), which together with turnover rates can be used to estimate litter production. The observed differences in ground vegetation type under the two tree species therefore indicates that litter from the ground vegetation contributed more to the total litter fall in pine forests than in spruce forests in southern Sweden, where a substantial part of the spruce plots lacked field layer altogether. For the cooler regions in the north, the ground vegetation type did not differ significantly between the two species since dwarf shrub types were dominant in both spruce and pine forests (Fig. 4).

The estimated inventory SOC stock to 1 m depth was based on information about the soil profile (horizon thicknesses etc.) and soil samples from four levels. The largest uncertainties were associated with the bulk density and volume of coarse fragments. The bulk densities was based on pedo-transfer functions (Nilsson and Lundin

2006), which rely on site specific data on C concentration and soil depths. The C concentration, which reflects organic matter content, is strongly related to bulk density, although it may depend on degree of soil compaction and soil texture as well. The largest uncertainty in SOC estimations in the mineral soil involves coarse fragments (Liski 1997, IPCC 2003), which is probably true for this study as well. The values used in this study were in accordance with a large-scale inventory of coarse fragment in Swedish forest soils by Stendahl et al. (2009), who reported on average 43% volume of coarse fragments in the upper 30 cm of the mineral soil. They also reported a significant correlation between surface boulder frequency and the volume of coarse fragments.

The simulations showed a relatively larger build-up of detrital and soil C for the spruce than for the pine stand (Fig. 5), which was similar in level to that of the SOC stock from the field data. However, when comparing results from the inventory SOC stocks with the simulated detrital and soil C stocks, attention must be paid to the fact that they represent different pools. Field data showed that the SOC stock in spruce plots was 20% larger than in the pine plots in the region where the simulations were carried out (Fig. 3; temperature sum class 1151–1350 degree days). This was fairly close to the simulated long-term difference of 22% for the SOC accumulated over several rotations. It should be noted that the simulation considered the combined detrital and soil C stocks accumulating from litter inputs over three rotations and 300 years, whereas the field data reports only soil C stocks including historic stores of carbon.

The simulation predicted larger biomass production in the spruce stand, although the rotation length was slightly shorter. The larger mean biomass carbon stock for spruce suggests that if the objective is to maximise this component, spruce should be used on this type of site. The difference in modelled combined detrital and soil C between spruce and pine stands at the end of the rotation can be attributed to differences in litter input at thinning and after clear-cutting. This input was much larger for spruce than for pine due to the larger standing biomass of spruce, but the difference in SOC stock between the two tree species will diminish in the decade following clear-cutting due to the fast decomposition rate of fresh litter. For both tree species, coarse woody litter contributed greatly to the accumulation of detrital and soil C (Fig. 6A–B), which was probably due to the fact that the simulation also included the non-humified component (litter/detritus).

In the simulation the initial soil C stock was assumed to be 0, and only detrital and soil C accumulated durng the ca 300 year simulation period was considered. For the comparisons between the tree species, the initial stock was assumed to behave similarly for spruce and pine stands in the comparisons between the species. There is little information available on the effect of tree species on stable mineral soil carbon pool though (Jandl et al. 2007). Other simulation studies comparing SOC under spruce and pine have shown similar differences. In a Finnish study where spruce and pine stands were simulated, the spruce had 24% more detrital and soil C after 150 years (Peltoniemi et al. 2004), while a Swedish simulation study reported that the spruce detrital and soil C was 35% larger after 150 years (Ågren and Hyvönen 2003).

Under spruce, thinnings and final fellings contributed more to the litter input than under pine, which resulted in more harvest residues remaining in the spruce stand compared with the pine stand. Therefore, removal of residues may have a greater impact on the SOC stock under spruce than pine stands. Removing harvest residues from final fellings for use as biofuel is common in Sweden, especially in southern and central areas, and contributes approximately 10 TWh year^{-1} (ca. 1 million tonnes C). It should be noted that it is more common to remove residues from spruce stands than from pine stands. Eriksson et al. (2007) found that the build-up of the SOC stock (including detritus) was reduced by 0.005 kg C m^{-2} year^{-1} for a spruce stand when residues were removed from the site. A more intensive use of the forest resource, extracting more biomass from the forest (e.g. for biofuel), may therefore reduce the SOC stock more in spruce than in pine forests.

In the simulated pine stand, the litter from the ground vegetation made an essential contribution to the build-up of the combined detrital and soil C stock, whereas in the spruce stand the input was much smaller (Fig. 6A–B). This was in accordance with the results from the field data, where sites lacking any field layer were more common for spruce than for pine plots, at least in the higher temperature sum regions. Furthermore, the contribution to the combined detrital and soil C stock from ground vegetation litter increased in the pine stand throughout the whole rotation, whereas for the spruce stand the contribution of ground vegetation decreased from the age of ca 20 years (Fig. 6A–B).

The simulation included several sub-models, which all contained uncertainties that may influence the conclusions. The forest model was based on long-term data from production experiments and is likely to provide robust results for forest development in the short term, although they might reflect historical production levels. Further, no feedback processes were included with respect, for example, changes to soil nutrient status or changing climate. The thinning interval and timing of harvesting were chosen more precisely than is normal practice, which might have resulted in higher production in the simulation than in reality, but was of the same magnitude for both tree species. Nevertheless, the higher productivity of spruce than of pine stands demonstrated in the current work was in agreement with Vollbrecht et al. (1995).

The estimates of litter production by different tree parts were based on biomass expansion functions and turnover rates. These were based on values representative of conditions in mid-Sweden and southern Finland. For below-ground litter it is difficult to verify the results since it is difficult to measure litter production directly, but for needle litter there is better data. Our comparison indicated a good agreement between our simulated needle litterfall rates with those calculated using empirical relationships derived using data from litterfall studies. It seems, however, that our simulation might underestimate needle litter production for the pine stand (by ca. 11%), in which case the difference between the two species would diminish.

The decomposition model assumed the same decomposition rate for spruce and pine needles, since any differences have not been sufficiently well quantified to be incorporated into the model. However, Johansson et al. (1986) found that spruce needle litter decomposes significantly slower than pine needle litter in paired stands of spruce and pine, growing on soils derived from the same bedrock in southern Sweden. This difference was attributed to differences in litter chemistry. If a slower decomposition rate for spruce needle litter was used for the simulation, then the combined detrital and soil C accumulation would have been even larger in the spruce compared to the pine stand.

This study shows that the choice of tree species could have a significant impact on the accumulation of detrital and soil C and could therefore be considered in the management of boreal forests. On sites where both Scots pine and Norway spruce are considered suitable, the latter should be selected if the aim of the forest management policy is to maximize the accumulation of carbon in the forest. The magnitude of accumulation will be affected by removals of residues for bioenergy. The impact of tree species is greater in areas of boreal forest where the temperature is low and on sites of low quality, but the accumulation of detrital and soil C is higher in areas where the temperature is high and on sites of high quality, irrespective of the selected tree species.

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