SILVA FENNICA

Silva Fennica 41(3) research articles

www.metla.fi/silvafennica · ISSN 0037-5330
The Finnish Society of Forest Science · The Finnish Forest Research Institute

# Carbon Sequestration Rates in Swedish Forest Soils – a Comparison of Three Approaches

Björn Berg, Per Gundersen, Cecilia Akselsson, Maj-Britt Johansson, Åke Nilsson and Lars Vesterdal

**Berg, B., Gundersen, P., Akselsson, C., Johansson, M.-B., Nilsson, Å. & Vesterdal, L.** 2007. Carbon sequestration rates in Swedish forest soils – a comparison of three approaches. Silva Fennica 41(3): 541–558.

Carbon sequestration rates in forest soil can be estimated using the concept of calculable stable remains in decomposing litter. In a case study of Swedish forest land we estimated C-sequestration rates for the two dominant tree species in the forest floor on top of the mineral soil. Carbon sequestration rates were upscaled to the forested land of Sweden with $23 \times 10^6$ ha with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (Karst.) L.). Two different theoretical approaches, based on limit-value for litter decomposition and N-balance for vegetation and SOM gave rates of the same magnitude. For the upscaling, using these methods, 17000 grids of 5×5 km were used.

The 'limit-value approach' gave a sequestration of $4.8 \times 10^6$ tons of C, annually sequestered in the forest floor, with an average of 180 kg C $ha^{-1} yr^{-1}$ and a range from 40 to 410 kg C $ha^{-1} yr^{-1}$. The 'N-balance approach' gave an average value of c. 96 kg $ha^{-1} yr^{-1}$ and a range from –60 to 360 kg $ha^{-1} yr^{-1}$. A method based on direct measurements of changes in humus depth over 40 years, combined with C analyses gave an average rate that was not very different from the calculated rates, viz. c. 180 kg $ha^{-1} yr^{-1}$ and a range from –20 to 730 kg $ha^{-1} yr^{-1}$. These values agree with forest floor C sequestration rate based on e.g. sampling of chronsequences but differ from $CO_2$ balance measurements.

The three approaches showed different patterns over the country and regions with high and low carbon sequestration rates that were not always directly related to climate.

**Keywords** stable humus, forest floor C, carbon sequestration, litter decomposition, limit value
**Addresses** *Berg*: Dept. of Forest Ecology, Univ. of Helsinki, Finland (present address: Dipartimento Biologia Strutturale e Funzionale, Complesso Universitario, Monte S. Angelo, Napoli, Italy; *Gundersen* & *Vesterdal*: Forest & Landscape Denmark, Univ. of Copenhagen, Denmark; *Akselsson*: Swedish Environmental Research Institute, IVL, Gothenburg, Sweden; *Johansson* & *Nilsson*: Dept. of Forest Soils, SLU, Uppsala, Sweden
**E-mail** bjoern.berg@unina.it, bjorn.berg@helsinki.fi
**Received** 15 August 2006 **Revised** 21 March 2007 **Accepted** 25 June 2007
**Available at** http://www.metla.fi/silvafennica/full/sf41/sf413541.pdf

# 1 Introduction

A long-term buildup of **s**oil **o**rganic **m**atter (SOM) takes place in forest ecosystems at undisturbed conditions. In a boreal forest, Wardle et al. (1997) found that thick mor humus (F+H) layers had accumulated for up to almost 3000 years under growing trees in undisturbed sites. This buildup of SOM based on remains from decomposing plant litter formed a C-sink in the order of 65 to 83 kg C/ha/yr. In present-day managed forests where fires are largely prevented such build ups may occur, although it is hard to measure due to soil heterogeneity as well as due to the lack of historic SOM data, that could form a reference for current measurements of soil C stocks.

Methods to quantify and upscale C sequestration in SOM are needed to better quantify global C-budgets as well as for national authorities to account for C sequestered in forest soils in the reporting of progress towards $CO_2$ reduction agreed in the Kyoto-protocol.

One approach to estimate C-sequestration in forest floor SOM has been proposed based on empirical models for decomposition (Berg et al. 2001). During litter decomposition a long-term stable fraction is formed (Berg et al. 2001, Berg and Dise 2004). One way to quantify stable remains is thus through studies of litter decomposition. The accumulated mass loss approaches a limit value, the level of which defines the stable remains (Berg and Ekbohm 1991, Berg et al. 1996). These remains mainly consist of lignified tissue (cf Berg and Matzner 1997), thus factors influencing the microbial lignin degradation such as litter N and Mn may control the stability and magnitude of the remains. The remaining fraction of stable organic matter is estimated from the calculated limit value for decomposition and multiplied by foliar litter fall to give the annual storage of SOM or C (Berg et al. 2001). This ‘limit value’ approach has been validated against the few existing datasets on forest floor SOM accumulation (Berg et al. 2001, Berg and Dise 2004) and procedures for upscaling have been developed and used on the Swedish forested area (Akselsson et al. 2005).

A second approach to estimate C sequestration was proposed by Gundersen et al. (2006) based on a quantification of the forest N balance. From the N balance, an estimate of soil N retention is derived and multiplied by the SOM C:N ratio to derive an estimate of soil C sequestration. For this approach upscaling procedures were also developed and applied for the Swedish forest area (Akselsson et al. 2007).

These two mainly theoretical approaches are, however, difficult to validate especially when extrapolated to regional or national level. But to this end a large Swedish dataset with measurements of forest floor depth from the 1960’s up to present day provides a possibility to compare calculated build up of organic layers with direct measurements of forest floor increase across Sweden. The changes in forest floor depth over 40 years can be converted to C sequestration rates and regionalized in an extrapolation procedure. Here we present a first summary and analysis of these data, which will be analyzed in more detail by Berg et al. (ms.).

The aim of this paper is to present and compare the above-mentioned three approaches for calculation of C sequestration rates in SOM scaled up to the forest area of Sweden. We compare the mean national estimates as well as the spatial patterns (on maps) of the three methods. The ‘limit value method’ calculates C sequestration rates in the forest floor and compares directly with C sequestration rates estimated from changes in the depth of forest floors, whereas the C sequestration rates calculated by the ‘N-balance method’ refer to SOM in the whole profile.

# 2 General Description on the Investigated Area

The region encompassed the forested land of the entire area of Sweden ranging from about 55ºN to 69ºN, with boreal climate north of c. 60ºN and a temperate climate from c. 55 to 60ºN. The mean annual temperature and precipitation varies from c. –2 to c. 8ºC and from 300 to 1100 mm, respectively. The gradient in precipitation generally follows that of the temperature decreasing from the south-west to the north. The forested area covers in all c. $23 \times 10^6$ ha, and the forests are mainly comprised of two coniferous tree species, Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). The deciduous species birch (silver birch, *Betula pendula* Roth and downy birch, *Betula pubescens* Ehrh.) is of significance whereas common beech (*Fagus sylvatica* L.), trembling aspen (*Populus tremuloides* Michx.) and common oak (*Quercus robur* L.) cover smaller areas. The annual N deposition ranges from c. 20 kg ha$^{-1}$ in the southwest to a basic value of c. 2 kg in the northern parts of the country according to data from 1998 from the MATCH model (Langner et al. 1996).

# 3 Materials and Methods

In this paper we use the term forest floor for the organic layer that develops on top of the mineral soil in most forest ecosystems. We calculate the forest floor C stock and forest floor C sequestration for this SOM layer, which is only a fraction of SOM-C in the whole soil profile.

### 3.1 Geographical Data Base

The basis for the calculations of C sequestration rates with the limit value and the N-balance methods was an extensive geographical database for Sweden with data on N deposition, land use, forest properties and hydrology. A detailed description of the data base has been published (Akselsson et al. 2005, 2007).

Four forest classes were used; coniferous forest, deciduous forest, mixed forest and clearcuts based on a satellite image (IRS WIFS) interpretation (Mahlander et al. 2004). Data about forest properties were derived from the SNFI (http://www-markinfo.slu.se). sites, managed by the Swedish University of Agricultural Sciences. Data on tree species composition (e.g. fractions of Norway spruce and Scots pine in coniferous forest), volume, growth and dry weight of different tree parts for coniferous, deciduous and mixed forests separately were Kriging interpolated to 17 000 grids, each of 5×5 km in the national coordinate system. The fraction of different tree species in the forest type classes was used to refine the landuse data. Based on these fractions, land covered by spruce, pine, and deciduous trees were calculated for each grid cell. All subsequent calculations were performed on a GIS platform with this resolution, which means that they were performed for each of the c. 17 000 grid cells of 5×5 km.

Runoff in the database was derived from a map from Swedish Meteorological and Hydrological Institute (SMHI, http://www.smhi.se), showing the annual mean runoff (1961–1990).

For the N-balance method we used additional values for modeled N deposition (nitrate plus ammonium) in the 5×5 km grids, using the dispersion model MATCH (Langner et al. 1996), which set the framework and resolution of the data base.

### 3.2 Limit Value Method

The *limit value approach* is based only on foliar litter fall since quantitatively correct measurements of non-foliar litter fall, such as woody components and cones, are rare. For the same reason we did not attempt to include data for root litter. Although the decomposition patterns for woody components are little known, available data and studies suggest that at least in natural boreal systems only small amounts of stable SOM are formed from them (Mark Harmon pers. comm.). We have considered foliar litter fall from mature stands only and the calculated values thus represent a potential for C sequestration of foliar litter input. Further, we did not consider the influence of a clear-cut phase or other forest management practices.

We have used limit values to calculate the stable remains (Berg and Ekbohm 1991) of decomposing litter using litter mass loss values. The limit value is the asymptotic value where the litter mass loss rate is zero or very close to zero. Limit values are available for the main litter species in Sweden. To calculate C sequestration rates in the forest floor over Sweden we used average limit values for mass loss of pine, spruce and deciduous foliar litter and calculated the remaining fraction using the function (100-limit value)/100 (Berg et al. 2001, Akselsson et al. 2005). We used three functions to predict foliar litter fall (pine, spruce, deciduous) as a function of actual evapotranspiration (AET) and calculated average values for each 5×5 km grid. We used two limit values for mass loss, one for Scots pine, Norway spruce and silver birch of 78% (a fraction of 0.22 as stable remains) and 64% for other deciduous trees, which equals a stable fraction of 0.36.

For upscaling we used AET values calculated as an average for each 5×5 km grid (Thorntwaite and Mather 1957) to calculate litter fall for each grid and species individually (Akselsson et al. 2005). The foliar litter fall (kg $ha^{-1}$ $yr^{-1}$) was multiplied by the corresponding area covered by Scots pine, Norway spruce or deciduous trees in each grid. The litter fall was divided by the total forest area in each grid (including clear-cuts) and multiplied by the fraction of stable remains (0.22 or 0.36) to set the accumulation rate of SOM in the forest floor (kg $ha^{-1}$ $yr^{-1}$). For further details see Akselsson et al. (2005).

### 3.3 N-balance Method

The N-balance method is based on the concept of stable litter remains and makes use of the generally close relationship between C and N in SOM and the fact that soil N accumulation can be estimated through mass balance calculations. Assuming that the C sequestration is proportional to the N accumulation and that the C:N ratio in the accumulating SOM is the same as the current C:N ratio in the forest floor, an estimate of the net C sequestration rate can be made by multiplying the accumulation of N in the soil by the C:N ratio of the forest floor, as proposed by Gundersen et al. (2006) (Eq 1):

$$C_{seq} < N_{acc} \times C{:}N_{forest\ floor} \qquad \text{(Eq. 1)}$$

where
$C_{seq}$ is the amount of C sequestered and
$N_{acc}$ the amount of N accumulated in the soil.

This is an upper estimate for the soil C sequestration rate since, especially at high N inputs, organic matter may accumulate at a lower C:N ratio than that of the current bulk forest floor mass. Further, some of the C is incorporated in SOM in the mineral soil where the C:N ratio usually is lower than in the SOM of the forest floor. The estimated C sequestration rates include the sequestration in the whole soil profile, thus both in forest floor and mineral soil. The forest floor C:N ratios used in the upscaling were derived using data from SNFI (Hägglund 1985). The regional C:N ratios are based on data from stands of different ages, and can thus be seen as averages for a forest rotation.

The soil N accumulation (Fig. 1) has been estimated through N mass balance calculations (Eq. 2) on a regional scale in Sweden (Akselsson and Westling 2005).

$$N_{acc} = N_{dep} + N_{fix} - N_{den} - N_{uptake} - N_{leach} \qquad \text{(Eq. 2)}$$

where
$N_{dep}$ = N deposition,
$N_{fix}$ = biological $N_2$ fixation, $N_{den}$ = N losses through denitrification,
$N_{uptake}$ = N losses through biomass harvest + N accumulated in vegetation through net growth and
$N_{leach}$ = N lost by leaching.

Nitrogen deposition values for different land use classes for the 1998 run of the MATCH model were used (Fig. 1). $N_2$ fixation was set to a low constant value of 1.5 kg $ha^{-1}$ $yr^{-1}$ based on a study by DeLuca et al. (2002). The denitrification was neglected since denitrification fluxes are known to be small in well-drained soils (Persson et al. 2000).

The N uptake (Fig. 1), here defined as the N removed from the system through harvest plus the N accumulating in the increasing standing biomass, was based on growth data. The internal circulation through uptake and litter fall was thus not included. The harvest intensity was quantified using province-based estimates of the fraction of the net growth that was harvested during the 1990s (Skogliga konsekvensanalyser 1999). Traditional forestry in Sweden implies harvest of stems only, but during the last decade whole-tree harvesting which includes removal of branches, tops and needles has become more common and increases N removal by harvest. This additional removal has not been considered in the present calculations. The N uptake thus corresponded to the N in the increasing standing biomass minus the N in the branches and needles that were left in the forest floor after the final felling. The estima-

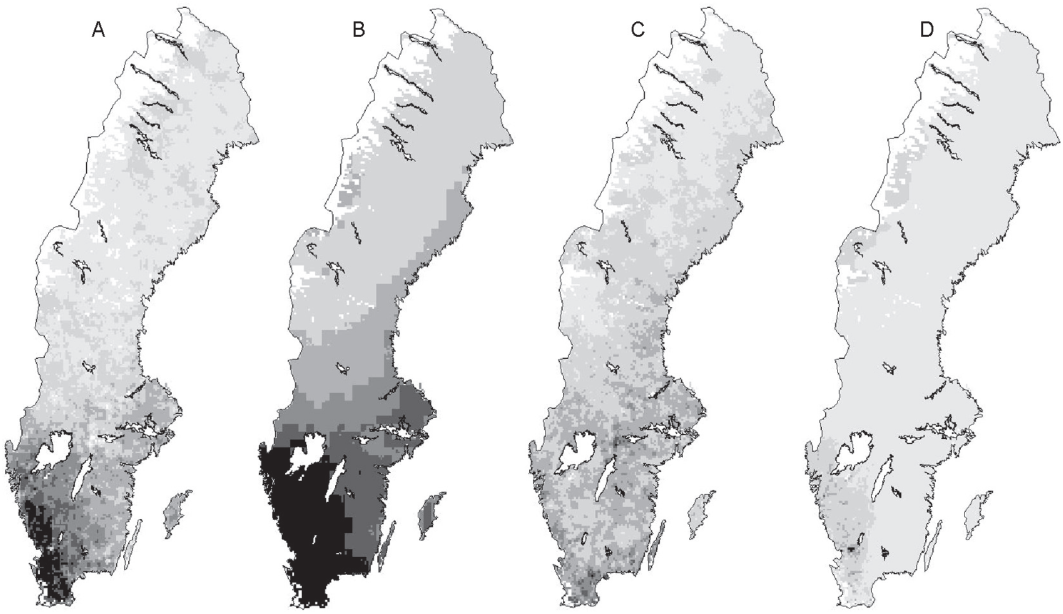


**Fig. 1.** Nitrogen dynamics over Sweden. A) N deposition, B) N losses through harvest plus N accumulated in trees through net growth, C) N leaching, D) N accumulation in soil from mass balance calculations. Dark shades = high values, vague shades = low values. Figure from Akselsson et al. 2007.

tions were based on net growth for the three main tree species and N concentrations in different tree parts (Akselsson et al. 2007).

Forest soils in Sweden normally have a high capacity to retain N (Nilsson et al. 1998) and the N leaching from soil under growing forests is accordingly low. The calculations of N leaching in this study (Fig. 1) were made for southern Sweden and central and northern Sweden separately, using different methods. The calculation of N leaching in central and northern Sweden was based on a study that related leaching of nitrate and organic N to runoff (Bergstrand et al. 2002, Brandt and Ejhed 2003). In southern Sweden where the N deposition is relatively high concentrations of inorganic N in soil water under clearcuts have been related to N deposition (Akselsson et al. 2004) and we used the positive linear regression function to calculate total N concentration in soil water under clearcuts in southern Sweden (Akselsson and Westling 2005). Nitrogen leaching was estimated by multiplying N concentration by water seepage flux.

By use of full rotation estimates for the parameters of the N balance (Eq. 2) as well as average forest floor C:N ratios (the average over stand ages, management differences etc), we include the effects of forest management in our estimates of C sequestration in SOM from this method.

### 3.4 Direct Measurement Approach

#### *3.4.1 General Design of the Forest Floor Inventory*

The changes in the thickness and C content of the forest floor layer for the period 1961–2001 were calculated using measured values from the Soil Survey and the National Survey of Forest Soils and Vegetation. We have used data from four inventories with annual measurements since 1961 covering over 40 years (http://www-markinfo.slu.se).

The basic units for measurements and samplings are sampling plots, which are organized in quadratic units, with a side ranging between 300 and 1800 m. Their frequency is highest in the southern parts of the country, with an average distance of 4 km, and lowest in the north where the minimum distance is 8 km. On each side of the unit are located four to seven circular sampling plots with a diameter ranging from 6.64 to 10 m among inventories.

We have used three groups of forest; i) dominated by Scots pine (>70% pine), ii) dominated by Norway spruce (>70% spruce), and iii) encompassing all combinations of species. The dominance is determined by the basal area in a given sampling plot.

Forest floor samples were taken with a 100-mm diameter soil corer and at least one core was taken from each sampling plot. Forest floor depth was measured in the hole, from the upper part of the bleached soil to the uppermost part of the F-layer in at least five holes around the sampled forest floor core. In each inventory between 9000 and 53 000 determinations of such average values were made. We have used 82 513 measurements of average forest floor depth, namely those on podzols as we limited the analysis to podzols and soils in which no B-horizon was formed.

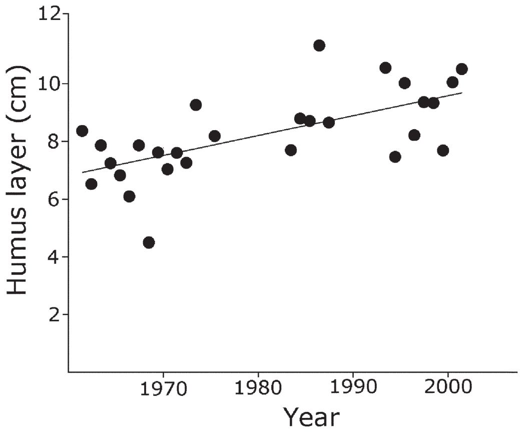


**Fig. 2.** Example of a linear relationship between time and the average value for humus thickness for one grid cell. In the case shown the linear relationship indicates an increase in humus-layer thickness from 7.0 to 9.1 cm in the period 1963–2001. This relationship calculated for a crossing point between grid plots represents a square of 25 × 25 km which has its center in the crossing point. We used in all 1794 such linear relationships

### *3.4.2 Sample Treatment and Chemical Analysis*

Each intact humus core was dried at room temperature, weighed, and its bulk density was calculated. In a next step roots were removed, the whole sample was homogenized and C analysed by dry combustion using an elemental analyser (LECO CNS-1000). Dry mass was determined on a subsample after drying over night at 105ºC.

### *3.4.3 Scaling up from Field Measurements in Plots to Country Level*

Due to the sampling patterns (above) we could not follow the development of the forest floor in single plots and we applied a scaling up procedure based on a modified Kriging interpolation and the national coordinate system, using grid cells of 25 × 25 km as the basic unit (RT90, http://www.lantmateriet.se). This procedure was similar to that for the 5 × 5 km grid cells (above), the only difference being that the cells were larger in this case.

To investigate for any change in the thickness of the forest floor over the 40-year period we calculated linear relationships between inventory year and the average values for forest floor depth for each 25 × 25 km grid cell (Fig. 2). This resulted in 1795 such relationships and we obtained 552, 602, and 641 relationships, for spruce-dominated and pine-dominated stands and for stands without species dominance, respectively.

### *3.4.4 Transfer of Change in Forest Floor Depth to C Sequestration Rate*

In the 1993–2001 inventory, each intact core was dried at room temperature, weighed, and its density was calculated. Roots were then removed, the sample was homogenized and C analysed by dry combustion using an elemental analyser (LECO CNS-1000). Dry mass was determined on a subsample after drying over night at 105ºC. To relate forest floor depth to amounts of C in the forest floor we used the surface of the soil corer and the bulk density of the sampled forest floor (kg $mm^{-1}$ $ha^{-1}$, Fig. 3B) from the 1993–2001 inventory to calculate the amount of SOM-FF stored. We determined forest floor density separately for the different tree classes. Finally we used the C concentration from the same sampling plot to calculate the amount of C stored using the C analyses. As we know i) the change in forest floor depth (Fig. 3A), ii) the C concentration in the forest floor (Fig. 3B) we can calculate iii) the rate at which forest floor C sequestration (Fig. 3C).

# 4 Results and Discussion

### 4.1 Carbon Sequestration Rates for the Three Approaches – Country Scale

The three different approaches gave rather similar average values for C sequestration rates. For the whole of Sweden the limit value approach gave an average of 180 kg C $ha^{-1}$ $yr^{-1}$ and a range from 40 to 410 kg C $ha^{-1}$ $yr^{-1}$ (Fig. 4). The N-balance approach gave 96 kg C $ha^{-1}$ $yr^{-1}$ and a range from –60 to 360 kg C $ha^{-1}$ $yr^{-1}$ (Fig. 6). Finally, the repeated forest floor inventory method gave an average rate of 180 kg C $ha^{-1}$ $yr^{-1}$ and a range from c. 0 to a main upper limit of 420 kg $ha^{-1}$ $yr^{-1}$ (Fig. 3C) with an extreme maximum of 717 kg $ha^{-1}$ $yr^{-1}$. Thus, three very different approaches resulted in average values of which two were almost identical and one c. 50% lower. In a modelling approach Liski et al. (2002) estimated C sequestration rates in forest soils (forest floor + the top 20 cm of the mineral soil) a.o. for Sweden and obtained an average value of 90 kg $ha^{-1}$ $yr^{-1}$, thus at the same level as the estimate based on the ‘N balance method’.

For the whole country both the limit-value approach and direct measurements gave an estimate of $4.8 \times 10^6$ tons of C sequestered annually, and N balance approach $2.2 \times 10^6$ (Fig. 6).

### 4.2 Patterns and Limitations of the Limit Value Method – All Tree Species

The calculations using limit values were based on litter fall related to AET, which gives a gradient in litter fall and thus in C sequestration rates with a decrease from the southwestern to the northern part of the country. In the southernmost part and on the west coast the C sequestration rates exceeded 300 kg $ha^{-1}$ $yr^{-1}$, in mid-Sweden the levels ranged mainly between 150 and 200 kg $ha^{-1}$ $yr^{-1}$ and in the northern parts the annual sequestration was lower than 100 kg $ha^{-1}$ with a minimum of 40 kg $ha^{-1}$ at and north of the Arctic Circle.

Foliar litter fall follows AET which thus becomes a strong factor for carbon sequestration rate (Fig. 4). AET spans from 375 mm in the northern part of Sweden to 540 mm in the southwestern part with higher temperature and more precipitation.

The present approach of this method assumes mature forests and does not account for clearcuts. We may express this so that it gives a potential for carbon sequestration from the foliar litter.

### 4.3 Patterns and Limitations in the N-balance Method

#### *4.3.1 Patterns in Carbon Sequestration Rates*

The C sequestration rates were highest in the south-western part of Sweden (Fig. 6). In the northern half of the country, rates were generally below 100 kg $ha^{-1}$ $yr^{-1}$.

The strong N deposition gradient drives the decreasing C sequestration from south to north. The estimates obtained with the ‘N balance method’ can be regarded as averages of soil C sequestration rates on the time-scale of a rotation in managed forests, since all stages of a rotation are included.

#### *4.3.2 Assumptions, Uncertainties and Limitations of the Method*

The calculations are not valid for ditched organic forest soils, corresponding to 7% of the managed forest area of Sweden (Hånell 1990). Thus, the total annual C sequestration may be somewhat overestimated, since organic forest soils after ditching become aerated, C mineralization starts and the soil layers may turn from sinks to sources.

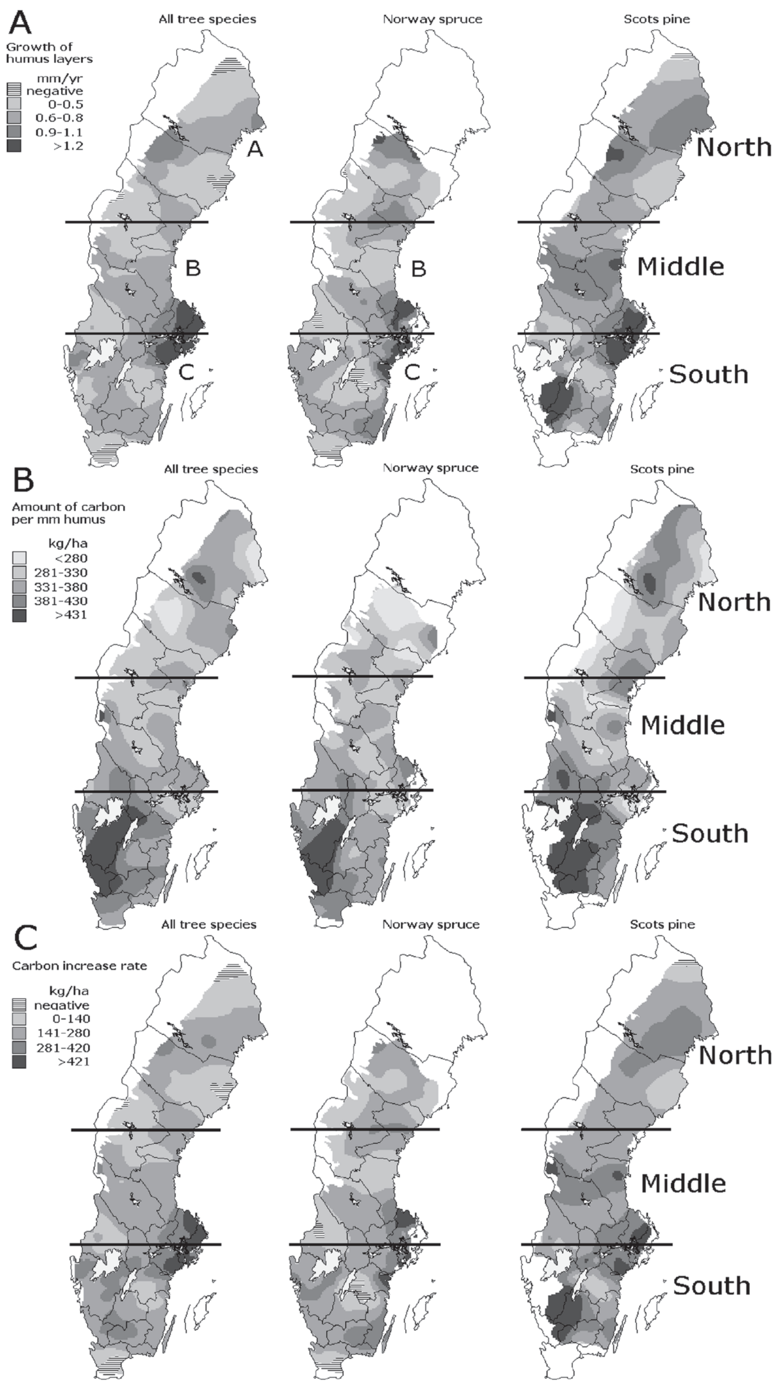


**Fig. 3.** A) Annual growth of humus layers, B) Amount of carbon per mm humus layer and hectare (carbon bulk density). C) Annual rate for carbon sequestration in the humus layer in Swedish forests in the period 1961 until 2001. The subdivision of the country into the three regions, North, Middle and South from north to the south is the same as shown in Fig. 7.

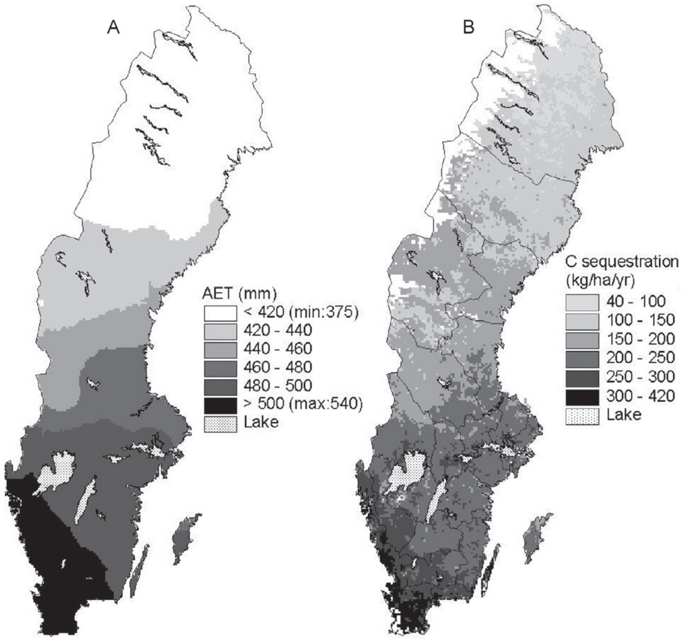


**Fig. 4.** A) Actual evapotranspiration in Sweden, based on a Kriging interpolation on 95 sites with modeled AET, using the Thornthwaithe and Mather (1957) water balance procedures. B) Carbon sequestration rates in the organic layers of forest soils in Sweden according to the limit-value method. Figure from Akselsson et al. 2005.

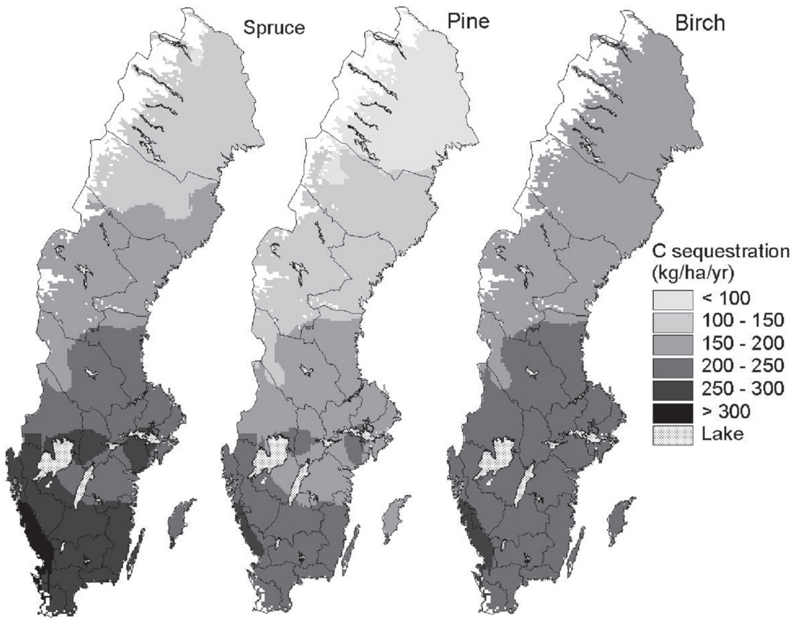


**Fig. 5.** Annual carbon sequestration rates in monocultural stands of Norway spruce, Scots pine, and birch spp. in different regions of Sweden. The sequestration rate was calculated using the limit-value method. The grid cell values are only valid for the specific tree species. Figure from Akselsson et al. 2005.

Different harvesting intensities as well as other forest management strategies can have a considerable effect on the C sequestration rates in forest soils (Liski et al. 1998, Ågren and Hyvönen 2003, Ericsson 2003). The calculation with the 'N balance method' in this study was based on conventional stem harvesting.

The overall uncertainty in the C sequestration calculations using this method is a result of the uncertainties in the estimated N accumulation and the assumption that the C:N ratio in the accumulating organic matter is the same as the C:N ratio in the existing organic layer in the soil. A rough approximation of the uncertainty in the N accumulation rate of ±1 kg $ha^{-1}$ $yr^{-1}$ gives a range in calculated C sequestration rates of ±20 kg $ha^{-1}$ $yr^{-1}$ in areas with low C:N ratios and ±40 kg $ha^{-1}$ $yr^{-1}$ in areas with high C:N ratios.

The assumption of the same C:N ratio in the accumulating organic matter as in the existing forest floor leads to uncertainties for two main reasons. Firstly, some of the C is accumulating in the mineral soil, which has a lower C:N ratio than the forest floor. The effect of this is, however, small, since most of the C is sequestered in the forest floor and the difference between the C:N ratio in the forest floor and the upper mineral soil is small. Secondly it is likely that the forest floor C:N ratio decreases with increasing N deposition, as indicated by several N fertilization studies (Nohrstedt et al. 2000, Prietzel et al. 2004). The close relationship between C and N in organic matter implies, however, that large and rapid changes of the C:N ratios are unlikely under prevailing N input conditions. Nohrstedt et al. (2000) evaluated the effects of N fertilization over a period of 28 years with dosages reaching up to as much as 86 kg $ha^{-1}$ $yr^{-1}$. The C:N ratio decreased significantly from 25 to 20 in the SOM of the forest floor with increasing N dosage. The long-term effects of N fertilization in Denmark were estimated by Beier and Eckersten (1998) using the SOILN model. With a dose of 35 kg N $ha^{-1}$ $yr^{-1}$ the C:N ratio decreased, from 31 to 28 over a 30-year period. The assumption of constant C:N ratios under increasing N deposition may be questionable, however, field studies have indicated that relatively large N input rates are needed to significantly decrease C:N ratios.

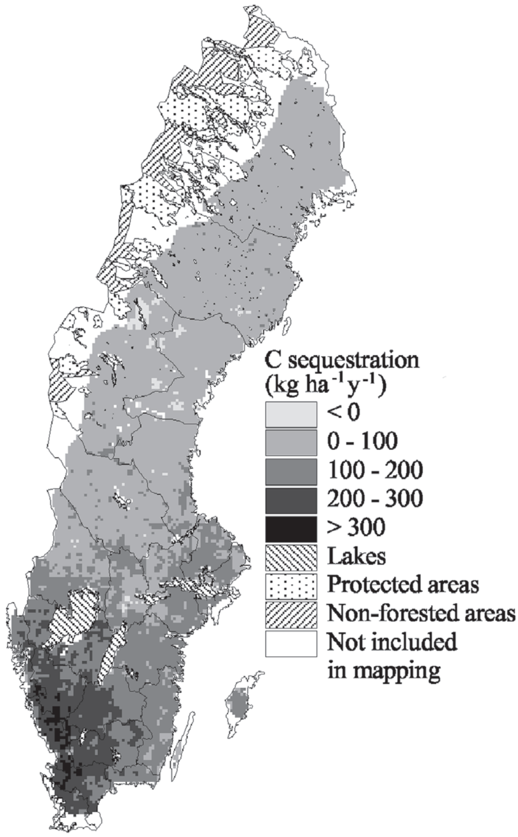


**Fig. 6** Carbon sequestration rates in Sweden (kg $ha^{-1}$ $yr^{-1}$) calculated using the 'N-balance method'. Figure from Akselsson et al. 2007.

## 4.4 Repeated Inventory of Forest Floor Depth – a Validation?

### *4.4.1 Change in Forest Floor Depth with Time*

As a first step we calculated linear relationships between inventory year and depth of the forest floor SOM for each 25×25km grid plot (Fig. 2). Within a dominant part of the country the linear relationships were significantly positive and practically all of the linear relationships for increasing forest floor depth showed a significant rate of increase ($p < 0.05$) (Table 1). For the spruce-dominated forest types, 531 of the 552 relationships were positive and 21 were negative.

**Table 1.** Numbers of significant linear relationships between humus depth and time. Three types of forest are identified based on dominant species. Dominance was determined using percentage of the total basal area as a measure. The number of linear relationships as well as positive and negative ones are given.

| Forest type | Fraction of the basal area | Linear relationships Total number | Positive | Negative |
|---|---|---|---|---|
| Spruce-dominated | >70% | 552 | 531 | 21 |
| Pine-dominated | >70% | 602 | 594 | 8 |
| All species[1)] | – | 641 | 604 | 35 |

[1)] Includes Scots pine, Norway spruce and deciduous trees

For the pine-dominated forest types 594 of the 602 relationships were positive and only 8 negative. Finally, for all species, 604 of the 641 relationships were positive and 35 were negative.

The reason for lack of significant relationships may vary on a very local basis. In northern Sweden part of the reason may be a methodological problem due to a too thin grid of sampling plots. In southern Sweden areas with a non-significant rate of increase included large afforested areas previously used for agriculture. Part of these areas were afforested with mainly Norway spruce after the first (1961–72) inventory adding sampling plots with either no or just thin forest floors which were registered in the following measurements and thus influencing the calculations. The slope of the relationship (Fig. 2) gave the increase rate in depth for the SOM-FF layer. We have used all 1794 relationships to produce a map for the increase rates in the SOM-FF layer thickness (Fig. 3A).

### *4.4.2 General Patterns in Forest Floor Depth Change – All Tree Species*

There is a general tendency for the average depth of the forest floor to increase with time. From an average of 7.47 mm (SD 8.52) in 1961 for the whole country (53 146 observations), the forest floor depth became 9.03 mm (SD 6.41) in 2001 (9305 observations) and the rates of change of forest floors ranged from c. 0.1 mm $yr^{-1}$ to > 1.2 mm $yr^{-1}$. Although there is a significant difference

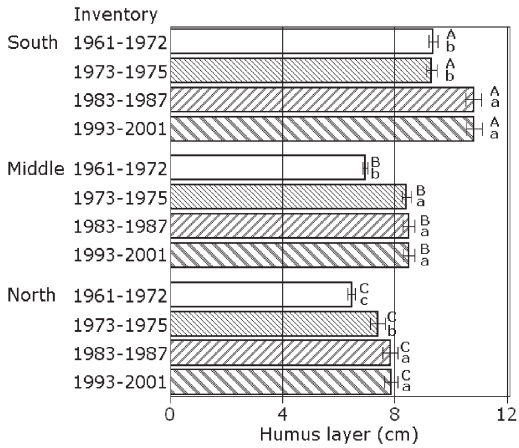


**Fig. 7.** Average humus-layer thickness in the four different inventories for three main regions of Sweden. Different capital letters indicate significant differences ($p < 0.05$) between the three regions for a given inventory. Different small letters indicate differences between inventories within the same region. The three regions are the same as those given in Fig. 3.

between the two averages, indicating a general tendency, the increasing is better distinguished when comparing data for three climatically different regions (North, Middle and South, Figs. 3A and 7). Using these regions which are taken arbitrarily in a first approach we may illustrate a general tendency, that the forest floors were deeper in the southern third of the country (9.4 cm) and the middle part with 6.9 cm as compared to the north with 6.45 cm already before the measurements started. The average forest floor depths were significantly different among the three regions.

After 40 years the humus layers had increased to an average of 10.8 cm in the south, which is significantly higher than in the first inventory. In the middle part the increase was significant (to 8.5 cm) as it was in the northern part (to 7.87 cm) (Fig. 7).

**Table 2.** Comparison of ranges and average values for three approaches in the present investigation with traditionally measured increase rates for C in soil organic matter, using e.g chronosequences and long-term measurements for specific plots on podzolic soils.

| Location | Sequestration rate (kg $ha^{-1}yr^{-1}$) Present investigation | Other investigations | Comment | Literature reference |
|---|---|---|---|---|
| Central Swedish Lapland | 141-280 | 77 | Mixed stands | (1, 3) |
| Central Sweden[A)] | 141-280 | 64 | Scots pine | (1, 4) |
| South Finland | | 47 | Norway spruce/Scots pine | (5) |
| Southwest Sweden[C, B)] | 280-420 | 650 | Norway spruce | (7) |
| Southwest Sweden/ Denmark[B] | 141-280 | 170-530 | Mixed stands | (2) |
| West Denmark (Jutland) | | 350 | Norway spruce | (7) |
| East Denmark (Sealand) | | 80 | Common oak | (6) |

[A)] Extremely nutrient-poor stand. [B)] Carbon sequestration rates in mainly deciduous forests in the southernmost part of Sweden are compared to values from Denmark using about the same latitude and considering a very similar climate. [C)] A coast-near site (called Tönnersjöheden)
(1) Berg et al. 2001, (2) Vesterdal and Raulund-Rasmussen 1998, (3) Wardle et al. 1997, (4) Staaf and Berg 1977, (5) Peltoniemi et al. 2004, (6) Vesterdal et al. 2002, (7) Vesterdal et al. 2007

#### *4.4.3 Bulk Density of the Forest Floor, Expressed as Carbon*

As a second step we calculated the bulk density of the forest floor, expressed as carbon (C bulk density), thus using a new concept. Defined as the amount of C per mm forest floor and hectare, we converted the increases in forest floor depth (Section 4.4.1) to C sequestration rates. When combining all forest types we found that the C bulk density varies over the country with a factor of c. 2. Considering all species, the highest density class was found in the southwestern parts of the country with > 431 kg C $mm^{-1}$ $ha^{-1}$ in an area with a high rainfall and a generally high N deposition. The least dense forest floors were found in the northern half of the country with < 280 kg C $mm^{-1}$ $ha^{-1}$ (Fig. 3B).

#### *4.4.4 Carbon Sequestration Rates and Some Patterns*

As a third step we calculated annual carbon sequestration. Using changes in forest floor depth (Fig. 3A) and C bulk density (Fig. 3B) we converted the depth change of the humus layer to annual C sequestraton for the 25×25 km grid plots. Using significant linear relationships (cf. Fig. 2) we obtained C sequestration rates ranging mainly between 140 and 420 kg C $ha^{-1}$ $yr^{-1}$ and with the average rate of 180 kg C $ha^{-1}$ $yr^{-1}$. The rate of C sequestration did not show any clear pattern over the country. Thus, in the northern parts we found areas with both low (< 140 kg C $ha^{-1}$ $yr^{-1}$) and relatively high (281–420 kg C $ha^{-1}$ $yr^{-1}$) C sequestration rates (Fig. 3C).

In three main areas carbon is lost, two in the southern parts of the country, both being afforested after use as farmland.

### 4.5 Comparison to Long-term Measurements Made in Single Stands

#### *4.5.1 Detailed Measurements in Sequestration Rates*

The high C sequestration rates for southern Sweden based on the N balance method and the limit value method may be supported by the direct measurements of Vesterdal and Raulund-Rasmussen (1998) and Vesterdal et al. (2002). For different sites they found C accumulation rates that ranged from c. 170 to ca 530 kg $ha^{-1}$ $yr^{-1}$. The climate in Denmark is very similar to that in southernmost Sweden and the data are therefore comparable. Although those experiments also included a changed land use it may still be used for a comparison.

For northern and central Sweden detailed measurements have given C sequestration rates of a magnitude of 65 to 83 kg C $ha^{-1}$ $yr^{-1}$ (Staaf and Berg 1977, Wardle et al. 1997), the former value originating from an extremely nutrient-poor pine forest in central Sweden, the latter from a richer mixed forest in Swedish Lapland.

Schulze et al. (2000) estimated the C sequestration rates in the soil at a forest stand in northern Sweden (Åheden, lat. c. 64ºN) and one in southern Sweden (Skogaby, lat. 56ºN). The estimated rates were 400–1400 kg $ha^{-1}$ $yr^{-1}$ and 1700–3000 kg $ha^{-1}$ $yr^{-1}$, respectively. Although these values are much higher than those reported in the present paper and by Vesterdal and Raulund-Rasmussen (1998), we cannot exclude that these estimates may be valid for the specific measurement years.

It deserves to be pointed out that in an area with high measured sequestration rates (> 421 kg C $ha^{-1}$ $yr^{-1}$) observed for all tree species and for Scots pine-dominated stands (Fig. 3C) it was reported from $CO_2$ balance calculations based on the whole soil column that the soil was a C source (Valentini et al. 2000). Our results, which in part are contradictory to these are well supported by all three approaches. Thus Akselsson et al. (2005) calculated for the same area a potential sequestration rate of 200–250 kg C $ha^{-1}$ $yr^{-1}$ for all species combined. Spruce is the dominant species in that area and the measured values for spruce-dominated forest ranged between 280 and 420 kg carbon $ha^{-1}$ $yr^{-1}$. Using the direct measurements, we found high sequestration rates (>420 kg C $ha^{-1}$ $yr^{-1}$). A reasonable explanation may be that there may be an extremely high carbon release from the lower part of the soil column that compensates for a high sequestration in the SOM-FF layer.

#### *4.5.2 Support for Long-term Stability*

Several measurements of forest floors in chronosequences and repeated samplings in growing stands indicate a linear increase with time for periods up to less than 100 years (e.g. Ovington 1957, 1959). Further, using published data (Wardle et al. 1997, Berg et al. 2001) we obtained a statistically significant linear relationship ($p < 0.01, n = 4$) between accumulated forest floor C and time for a period between 120 and 2984 years, suggesting that the C sequestration rate was rather constant. This also means that no steady state was indicated below 3000 years or below a total carbon accumulation of 250 000 kg C $ha^{-1}$ in the organic layer, further supporting a stable increase. These observations were made in forests with undisturbed soils. The sequestered amounts of carbon were reconstructed by Berg et al. (2001) and by Berg and Dise (2004) using the limit-value concept in which a recalcitrant fraction is calculated using actual litter decomposition data.

Using this information we may speculate that the undisturbed forest floor under a growing forest may have a certain long-term stability. That the humus layers grow and reach such a high amount of sequestered carbon as 250 000 kg $ha^{-1}$ is in clear contrast to the concept of steady state for forest floors, often used in critical load calculations for example by Schulze et al. (1989) who claimed that there would be no significant growth of forest floors over Sweden.

The concept humus may encompass carbon of different decomposability. We may use a subdivision of FH-layer humus presented by Couteaux et al. (1998), which is functional from the point of view of degradability. They divided the humus into three fractions based on degradation rate, namely labile, intermediate and resistant. The latter part encompassed ca 91% of the H-layer humus and had a decomposition rate of 1% mass loss in 30 to 300 years, whereas the labile part made up ca 0.00% of the same layer and the intermediate fraction only 9.8% and had a degradation rate ca 100 times higher than the resistant part. This study thus supports that a main part of the forest floor may be long-term recalcitrant.

The method based on direct measurements of humus depth presented in this paper covers both undisturbed areas and areas affected by forest management, such as site preparation. Thus the results include both undisturbed and heavily disturbed areas. Still the carbon sequestration rate as determined in the present study has an average value that is very close to that obtained by Akselsson et al. (2005), namely 180 kg C $ha^{-1}$ $yr^{-1}$, a value calculated as a potential, assuming only mature undisturbed stands.

### 4.6 Comparison of the Three Methods

#### *4.6.1 Comparisons of All Tree Species Combined*

Validations of regional estimations are difficult to perform with any accuracy. The uncertainties in the different calculation steps can be quantified and discussed to some extent, as described above. For a more satisfactory validation the final results should be compared to estimations of C sequestration obtained by other methods and we have applied three methods, of which two can be considered as theoretical and one in which we used direct measurements of SOM-FF layer depth.

The two theoretical calculations of C sequestration, based on entirely different methods, showed the same main gradient with decreasing C sequestration rates from the southwestern to the northern part of the country (Figs. 2 and 6). Carbon sequestration in the forest floor layer, calculated with the 'limit value method', spanned from 40 to 410 kg $ha^{-1}$ $yr^{-1}$ (Fig. 2). This approach does not give negative values and we may consider it to show a potential sequestration rate, let be that so far only foliar litter fall is used. The corresponding interval for C sequestration rates using the 'N balance method' was –60 to 350 kg $ha^{-1}$ $yr^{-1}$ (Fig. 6) and for the repeated inventory approach, mainly 0 to 420 kg $ha^{-1}$ $yr^{-1}$. Some single extremes deviate from the main pattern. Still the values obtained with the three different methods close to those for careful, long-term measurements in single stands and chronosequences.

For the southwestern part of the country, both theoretical estimations showed clear similarities, both with high C sequestration rates with 410 and 350 kg C $ha^{-1}$ $yr^{-1}$ for the limit value method and the N-balance method, respectively. The direct measurements gave somewhat lower values in the range 141–280 kg C $ha^{-1}$ $yr^{-1}$ and for some areas with the range 281–420 kg C $ha^{-1}$ $yr^{-1}$. For northern Sweden the 'N balance method' ranged from –60 to 110 kg $ha^{-1}$ $yr^{-1}$ and the limit value method from 40 to 200 kg $ha^{-1}$ $yr^{-1}$, whereas the direct measurements gave about equal areas with 0–140 and 141–280 kg C $ha^{-1}$ $yr^{-1}$.

Available data (Section 4.5.2) suggest a real long-term stability and even question the concept 'steady state'. If we consider that possibility we may speculate why a method based on foliar litter fall only, gives C sequestration rates similar to a method based on all litter inflows, namely the repeated inventory method. Would the foliar litter fraction be dominant from the point of view of carbon sequestration irrespective of litter inflows from roots and woody litter fall? Alternatively – would forest management which is not addressed by the limit value method, but in the direct measurements' method have such a high negative effect on carbon sequestration thus decreasing it so it becomes comparable to what is calculated from only foliar litter using the limit-value method?

We have emphasized that the methods are clearly different. Still two have given about identical values and the third a value about 50% lower. Further, a difference in about 90 kg C/ha/yr indicates that the sequestration values we have calculated are in the correct range.

#### *4.6.2 Different Carbon Sequestration Rates among Tree Species*

The different approaches gave somewhat different patterns in sequestration rates that could be related to forest type and tree species.

In the limit-value approach foliar litter fall was an influential factor and foliar litter fall is generally higher in spruce than in pine forests (Akselsson et al. 2005), which in our approach results in a higher annual mean C sequestration in spruce than in pine forests with averages of 200 kg $ha^{-1}$ and 150 kg $ha^{-1}$, respectively. The mean C sequestration rate in birch forests is the same as for pine, but the gradient over Sweden is more emphasized in pine forests with a wider range (60 to 260 kg $ha^{-1}$ $yr^{-1}$) than for birch (150 to 260 kg $ha^{-1}$ $yr^{-1}$) (Fig. 5).

Akselsson et al. (2005) used a common limit value for Scots pine, Norway spruce and birch spp with 78% and thus a stable fraction of 0.22. The litter class with 'other deciduous trees' was limited to the southern part of Sweden and has the lowest limit value with 64% and thus a stable fraction of 0.36, which has given a C sequestration rate of about 400 kg $ha^{-1}$ $yr^{-1}$, which was higher than for spruce, pine and birch litter with a smaller stable fraction. This effect can be seen in parts of southernmost Sweden (Fig. 1) where forests of common beech and common oak make up a significant fraction of the forested area, or 22% of the standing volume in the southernmost province (Statistical yearbook of forestry 2003).

Using the direct measurements' method we obtained clear differences among forest types. Thus for spruce-dominated forests the rate was on the average 178 kg C $ha^{-1}$ $yr^{-1}$ (SD = 123), and for pine-dominated it was 263 kg C $ha^{-1}$ $yr^{-1}$ (SD = 141). For all species the rate was 176 kg C $ha^{-1}$ $yr^{-1}$ (SD = 110). The difference of 84 kg C $ha^{-1}$ $yr^{-1}$ between pine and spruce forests was highly significant and calculated using 506 grid plots that allowed a more precise comparison.

The maximum C sequestration rates were 717, 714 and 561, respectively for spruce, pine and mixed forests. Areas with high rates were clearly more frequent in pine-dominated as compared to spruce-dominated forests. Pine-dominated forests in the southwestern parts showed a very high increase rate for sequestered carbon with >430 kg C $ha^{-1}$ $yr^{-1}$. Also in pine forests in the eastern parts of mid-Sweden the increase rate was high with 290 to 430 kg C $ha^{-1}$ $yr^{-1}$.

Spruce-dominated forests showed a very different pattern as compared to pine and we found only some small areas with sequestration rates higher than 421 kg C $ha^{-1}$ $yr^{-1}$, located in eastern mid-Sweden.

We may compare the averages using the two methods. The limit value approach was strongly related to foliar litter fall which is generally higher in Norway spruce than in Scots pine forests (Akselsson et al. 2005), resulting in a higher annual mean C sequestration in spruce than in pine forests with 200 kg $ha^{-1}$ and 150 kg $ha^{-1}$, respectively (Fig. 5). We may speculate that the moss and lower shrubs may be of importance in the more open pine forests giving significant additions to the litter input. Norway spruce forests generally have a denser canopy cover than those with pine, often without moss and with less shrubs such as cowberry, bilberry and heather, which in part may explain the difference. The carbon sequestration rates for spruce forest were 178 kg $ha^{-1}$ $yr^{-1}$ in the direct measurements' approach and 200 kg $ha^{-1}$ $yr^{-1}$ for the limit value approach giving a difference of 22 kg. For pine forests the rates were 263 and 150 kg $ha^{-1}$ $yr^{-1}$, respectively, and the larger difference of 113 kg C may give a support for such an extra source of litter.

# 5 Conclusions

The amount of carbon sequestered in humus increases in forests and it appears that the average rate for Sweden is of the magnitude 100 to 200 kg C $ha^{-1}$ $yr^{-1}$. The similarities in general sequestration rates between three very different methods is a good support for this. Combining the information from the limit value approach and the humus-depth measurements we may speculate in that the potential accumulation may be higher than suggested by the present studies.

The clearly higher measured total sequestration rates in Scots pine forests indicates that the reason to the difference between Scots pine and Norway spruce stands should be further investigated. Further, the similarity in sequestration rates between the limit value method, which gives a potential, using only foliar litter and the method based on changing humus depth, considering litter production and all management effects indicates the necessity to investigate what litter components that really produce stable remains.

# Acknowledgements

The thorough work and comments of two anonymous referees is gratefully acknowledged.

# References


Ågren, G. & Hyvönen, R. 2003. Changes in carbon stores in Swedish forest soils due to increased biomass harvest and increased temperatures analyzed with a semi-empirical model. Forest Ecology and Management 174: 25–33.

Akselsson, C. & Westling, O. 2005. Regionalized nitrogen budgets in forest soils for different deposition and forestry scenarios in Sweden. Global Ecology and Biogeography 14: 85–95.

— , Westling, O. & Örlander, G. 2004. Regional mapping of nitrogen leaching from clearcuts in southern Sweden. Forest Ecology and Management 202: 235–243.

— , Berg, B., Meentemeyer, V. & Westling, O. 2005. Carbon sequestration rates in organic layers of boreal temperate forest soils – Sweden as a case study. Global Ecology and Biogeography 14: 77–84.

— , Westling, O., Sverdrup, H. & Gundersen, P. 2007. Nutrient and carbon budgets in forest soils as decision support in sustainable forest management. Forest Ecology and Management 238: 167–174.

Beier, C. & Eckersten, H. 1998. Modelling the effects of nitrogen addition on soil nitrogen status and nitrogen uptake in a Norway spruce stand in Denmark. Environmental Pollution 102: 409–414.

Berg, B. & Dise, N. 2004. Validating a new model for N sequestration in forest soil organic matter. Water, Air and Soil Pollution: Focus 4(2–3): 343–358.

— & Ekbohm, G. 1991. Litter mass-loss rates decomposition patterns in some needle leaf litter types. Long-term decomposition in a Scots pine forest VII. Canadian Journal of Botany 69: 1449–1456.

— & McClaugherty, C. 2003. Plant litter. Decomposition, humus formation, carbon sequestration. Springer Verlag Heidelberg, Berlin. 296 p.

— & Matzner, E. 1997. Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environmental Reviews 5: 1–25.

— , Ekbohm, G., Johansson, M.-B., McClaugherty, C., Rutigliano, F. & Virzo De Santo, A. 1996. Some foliar litter types have a maximum limit for decomposition – a synthesis of data from forest systems. Canadian Journal of Botany 74: 659–672.

— , McClaugherty, C., Virzo De Santo, A. & Johnson, D. 2001. Humus buildup in boreal forests – effects of litter fall and its N concentration. Canadian Journal of Forest Research 31: 988–998.

— , Johansson, M.-B., Nilsson, Å., Gundersen, P. & Norell, L. 200X. Sequestration of carbon in soil organic matter layers in Swedish forests – direct measurements. Global Ecology and Biogeography (Manuscript, submitted).

Bergstrand, M., Brandt, M., Arheimer, B., Grahn, G., Gyllander, A., Pers, C., Svensson, P., Ejhed, H., Johnsson, H., Olsson, K., Mårtensson, K., Löfgren, S. & Westling, O. 2002. TRK – nutrient load in Sweden – an operational system for catchment modelling of nutrient transport, retention and source apportionment. In: Killingtveit, Å. (ed.). Proceedings of Nordic Hydrologic Programme (NHP), Report 47(1): 211–220. Nordic Association of Hydrology, Röros, Norway.

Brandt, M. & Ejhed, H. 2003. TRK Transport – Retention – Källfördelning. Belastning på havet. Swedish Environmental Protection Agency, Report 5247. 44 p. (In Swedish).

Couteaux, M.-M., McTiernan, K., Berg, B., Szuberla, D. & Dardennes, P. 1998. Chemical composition carbon mineralisation potential of Scots pine needles at different stages of decomposition. Soil Biology and Biochemistry 30: 583–595.

DeLuca, H., Zackrisson, O., Nilsson, M.-C. & Sellstedt, A. 2002. Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419: 917–920.

Ericsson, E. 2003. Carbon sequestration and fossil fuel substitution during different rotation scenarios. Scandinavian Journal of Forest Research 18: 269–278.

Gundersen, P., Berg, B., Currie, W.S., Dise, N.B., Emmett, B.A., Gauci, V., Holmberg, M., Kjønaas, J., Mol-Dikstra, J., van der Salm, C., Schmidt, I.K., Tietema, A., Wessel, W.W., Vestgarden, L.S., Akselsson, C., De Vries, W., Forsius, M., Kros, H., Matzner, E., Moldan, F., Nadelhoffer, K.J., Nilsson, L.-O., Reinds, G.J., Rosengren, U., Stuanes, A. & Wright, R.F. 2006. Carbon-nitrogen interactions in forest ecosystems – final report. Forest and Landscape, KVL. Working Papers 17. Forestry. ISBN 978-877903-287-3.

Hägglund, B. 1985. A new Swedish national forest survey. Swedish University of Agricultural Sciences, Report 37, Uppsala, Sweden. (In Swedish with English summary).

Hånell, B. 1990. Torvtäckta marker, dikning och sumpskogar i Sverige. Skogsfakta 22. Swedish University of Agricultural Sciences, Uppsala, Sweden. (In Swedish).

Langner, J., Persson, C., Robertson, L. & Ullerstig, A. 1996. Air pollution assessment study using the MATCH modelling system. Application to sulphur and nitrogen compounds over Sweden 1994. Swedish Meteorological and Hydrological Institute, Report 69.

Lantmäteriet. Available at http://www.lantmateriet.se (cited 24 January 2006).

Liski, J., Ilvesniemi, H., Mäkelä, A. & Starr, M. 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. European Journal of Soils Science 49: 407–416.

— , Perrechoud, D. & Karjalainen, T. 2002. Increasing carbon stocks in the forest soils of western Europe. Forest Ecology and Management 169: 159–175.

Mahlander, C., Hellsten, S., Akselsson, C. & Ekstrand, S. 2004. National land cover mapping for air pollution studies. IVL Report B-1499. 19 p.

Nilsson, S.I., Berggren, D. & Westling, O. 1998. Retention of deposited $NH_4$-N and $NO_3$-N in coniferous forest ecosystems in southern Sweden. Scandinavian Journal of Forest Research 13: 393–401.

Nohrstedt, H.-Ö., Jacobson, S. & Sikström, U. 2000. Effects of repeated urea doses on soil chemistry and nutrient pools in a Norway spruce stand. Forest Ecology and Management 130: 47–56.

Ovington, J.D. 1957. Dry-matter production by Pinus sylvestris L. Annals of Botany 21(2): 287–314.

— 1959. The circulation of minerals in plantations of Pinus sylvestris L. Annals of Botany 23(2): 229–239.

Peltoniemi, M., Mäkipää, R., Liski, J. & Tamminen, P. 2004. Changes in soil carbon with stand age – an evaluation of a modeling method with empirical data. Global Change Biology 10: 2078–2091.

Persson, T., Rudebeck, A., Jussy, J.H., Colin-Belgrand, M., Priemé, A., Dambrine, E., Karlsson, P.S. & Sjöberg, R.M. 2000. Soil nitrogen turnover – mineralisation, nitrification and denitrification in European forest soils. In: Schulze, E.-D. (ed.). Carbon and nitrogen cycling in European forest ecosystems. Springer, Ecological Studies 142: 297–231.

Prietzel, J., Wagoner, G. & Harrison, R. 2004. Long-term effects of repeated urea fertilization in Douglas-fir stands on forest floor nitrogen pools and nitrogen mineralization. Forest Ecology and Management 193: 413–426.

Schulze, E.-D., de Vries, W., Hauhs, M., Rosen, K., Rasmussen, L., Tamm, C.O. & Nilsson, J. 1989. Critical loads for nitrogen deposition on forest ecosystems. Water, Air and Soil Pollution 48: 451–456.

— , Högberg, P., van Oene, H., Persson, T., Harrison, A.F., Read, D., Kjøller, A. & Matteucci, G. 2000. Interactions between the carbon and nitrogen cycles and the role of biodiversity: a synopsis of a study along a north-south transect through Europe. In: Schulze, E.-D. (ed.). Carbon and nitrogen cycling in European forest ecosystems. Springer, Ecological Studies 142: 468–491.

Skogliga konsekvensanalyser 1999. National Board of Forestry. Report 2:2000. (In Swedish). ISSN 1100-0295.

Staaf, H. & Berg, B. 1977. A structural and chemical description of litter and humus in the mature Scots pine stand at Ivantjärnsheden. Swedish Coniferous Forest Project, Internal Report 65. 31 p.

Statistical Yearbook of Forestry 2003. Skogsstyrelsen, Sweden. (In Swedish).

Swedish Meteorological and Hydrological Institute. Available at http://www.smhi.se (cited 24 January 2006).

Swedish University of Agricultural Sciences. Available at http://www-markinfo.slu.se (cited 24 January 2006).

Thornthwaite, C.W. & Mather, J.R. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology 10: 185–311.

Valentini, R., Mattelucci, G., Dolman, A.J., Schulze, E.-D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Mundsson, J.G.U., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Mongriff, K., Montagnani, L., Minerbi, S. & Jarvis, P.G. 2000. Respiration as the main determinant of carbon balance in European forests. Nature 404: 861–865.

Vesterdal, L. & Raulund-Rasmussen, K. 1998. Forest floor chemistry under seven tree species along a soil fertility gradient. Canadian Journal of Forest Research 28: 1636–1647.

— , Ritter, E. & Gundersen, P. 2002. Change in organic carbon following afforestation of former arable land. Forest Ecology and Management 169: 137–147.

— , Rosenqvist, L., van der Salm, C., Hansen, K., Groenenberg, B.-J. & Johansson, M.-B. 2007. Carbon sequestration in soil and biomass following afforestation: experiences from oak and Norway spruce chronosequences in Denmark, Sweden and the Netherlands. In: Heil, G.W., Muys, B. & Hansen, K. (eds.). Environmental effects of afforestation in North-Western Europe – field observations to decision support. Springer, Plant and Vegetation 1: 19–52.

Wardle, D.A., Zachrisson, O., Hörnberg, G. & Gallet, C. 1997. The influence of island area on ecosystem properties. Science 277: 1296–1299.

*Total of 46 references*