Carbon and Nitrogen in Danish Forest Soils—Contents and Distribution Determined by Soil Order

Henrik Vejre,* Ingeborg Callesen, Lars Vesterdal, and Karsten Raulund-Rasmussen

ABSTRACT

Increasing atmospheric CO₂ concentrations, and widespread deposition of N to terrestrial ecosystems has increased the focus on soil C and N pools. The aim of this study was to estimate the size and distribution of organic C and N pools in well-drained Danish forest soils. We examined 140 forest soil profiles from pedological surveys of Danish forest soils. We calculated total C and N pools in organic layers and mineral soils to a depth of 1 m. The profiles represent variations in texture (sandy to loamy), and soil order (USDA soil taxonomy Spodosols, Alfisols, Entisols, and Inceptisols). The average total organic C and N contents were 12.5 and 0.61 kg m⁻² respectively. There were large differences in total C and N among soil orders. Spodosols had the greatest C content (14.6 kg m⁻²), and Alfisols the least (8.8 kg m⁻²), while the N content was highest in Alfisols (0.75 kg m⁻²) and least in Spodosols (0.51 kg m⁻²). The main contributor to the high C content in Spodosols is the spodic horizons containing illuvial humus, and thick organic horizons. Carbon and N concentrations decreased with soil depth. Soil clay content was negatively correlated to C content and positively correlated to N content. Soil order and horizon designations may be useful in predicting the total C and N content of Danish forest soils, and may also predict potential for C sequestration following afforestation of arable land.

The increasing concentration of atmospheric CO₂ has directed focus on global C cycles and pools. Atmospheric and oceanic compartments of global C budgets have attracted the most attention, while terrestrial systems have been treated as a near neutral compartment (Eswaran et al., 1995). Because terrestrial ecosystems constitute major C sinks this has proven inadequate in accounting for all global C sources and sinks. Several studies have suggested that soils represent a substantial C compartment (Murillo, 1994; Westman et al., 1994). In ecosystems where net primary production exceeds decomposition, net C accumulation takes place, in living biomass above and below ground and in organic matter in the forest floor (O horizons) and soil. Soils may act as significant C sinks because of the accretion of soil organic matter (SOM) (Eswaran et al., 1995; Cannell and Milne, 1995). Soil C pools may exceed aboveground terrestrial biomass C pools by up to three times (Eswaran et al., 1993).

Biomas in living plants is accumulated by the autotrophic synthesis of organic compounds. This process incorporates both C and N in the living biomass making the two elements intimately associated in both living and dead organic material. Because of this relationship the C/N ratio is used to characterize living and dead organic matter. The total C accumulated in biomass is generally limited by the availability of N. Forest trees are often adapted to N limited conditions by mechanisms that exert tight controls on the N cycles (Melillo, 1981; Aber et al., 1989). In these N limited ecosystems, increased supplies of plant available N from deposition may result in increased biomass production, and consequently additional fixation of C (Mäkipää et al., 1999). Holland et al. (1997) estimated that N deposition alone might allow for the sequestration of an additional 1.4 × 10³ to 2 × 10³ Mg C yr⁻¹ worldwide. Therefore, N input was seldom considered harmful in terms of biomass production. However, since the early 1980s, the focus has been on the negative impacts of deposition of atmospheric N in forest ecosystems (Gundersen and Rasmussen, 1995), including acidification, induction of nutrient deficiencies, leaching of essential nutrients and harmful elements, requiring attention and countermeasures (Skeffington, 1990).

Soil organic matter may diminish because of changes in climate, land use, and land management (Harrison et al., 1995; Murillo, 1994; Schlesinger, 1995; Lal et al., 1995). The size of the annual input of organic material and decomposition rates are key factors regulating SOM pool sizes. Because these factors depend on forest productivity and soil fertility, soil properties are the primary factor determining the C content of forest soils within climatic regions (same moisture and temperature regimes as proposed by Soil Taxonomy) (Tate, 1992; Eswaran et al., 1995).

The role of SOM as a C and N reservoir, the sensitivity of SOM to environmental changes, and the use of C/N ratios as an indicator of ecosystem stability have necessitated precise estimations on the soil C and N pools worldwide.

Our objective in this study was to estimate the size and distribution of organic C and N pools in well-drained Danish forest soils. We gathered all data available; soil profiles characteristics, and chemical and physical variables that are related to C and N storage in soils, we then analyzed and discussed these data to establish relationships with soil forming processes.

We examined hypotheses concerning the relationship between accumulation of C and N and soil order; and soil order differences in C and N concentration and C/N ratio changes with soil depth. Further, we examine whether the forest floor C and N storage is influenced by soil order.

H. Vejre, Centre for Forest, Landscape and Planning, Royal Veterinary and Agricultural University; DK-1871 Frederiksberg C, Denmark; I. Callesen, L. Vesterdal, and K. Raulund-Rasmussen, Centre for Forest, Landscape and Planning, Danish Forest and Landscape Research Institute, Hørsholm Kongevej 11 DK-2970 Hørsholm, Denmark. Received 26 June 2001. *Corresponding author (hv@kvl.dk).


Abbreviations: SOM, soil organic matter.
MATERIAL AND METHODS

Study sites

Denmark is located at approximately 56° N long. and 10° E lat. The present climate of Denmark is characterized by an udic moisture and mesic temperature regime (Soil Survey Staff, 1992). Precipitation ranges from 600 through 1000 mm yr⁻¹ and the mean annual temperature is 7.5°C. During the Pleistocene, Denmark was heavily glaciated after which soil formation commenced. The climate in Denmark has changed several times since the end of the Pleistocene (10,000 BP) (Iversen, 1973). These early climatic conditions along with present climate are factors in the variation in Danish soil properties. For soil formation discussions, Denmark may be considered uniform in macroclimate. The Danish terrain is level to undulating, and maximum elevation is 173 m above sea level (m.a.s.l). The main geologic features include Cretaceous limestone and Tertiary clays and sand, which modified by several glacial events, gave rise to the present landscape of moraines and glaciofluvial plains, with common marine and eolian deposits. Accordingly, the soils developed on loamy and sandy glacial till, glaciofluvial, marine, and eolian sand (Hansen, 1965).

Data Acquisition

Data for this study were acquired from 140 forest soil profiles from pedological surveys performed between 1970 and 1998 (Dalsgaard et al., 1981; Dalsgaard et al., 1991; Raulund-Rasmussen, 1993; Breunig Madsen and Olsson, 1995; Raulund-Rasmussen and Vejre, 1995; Vesterdal et al., 1995; Vejre and Hoppe 1998; Vesterdal and Raulund-Rasmussen 1998). Soil profile data included in this study had: detailed profile description, samples collected in pedogenic horizons, total C or N data, and exact location mapped. Precise profile description and horizon depth allowed classification to soil order according to Soil Taxonomy (Soil Survey Staff, 1992). All sites were forested and classified as moderately well drained or better, to avoid hydromorphic and organic soils. See Figure 1 for site locations. Most sites were plantation forests, except 22 sites located in semi-natural or managed beech (Fagus Silvatica L.) forest; all had been forested for the last 100 yr. All sites were located in flat (<1% slope) to undulating

Fig. 1. Map of Denmark showing sites and soil order.
(5–10% slope) terrain. Sites influenced by erosion or strong variations in hydrological regimes were not included.

**Soil Analysis and Classification**

A total of 106 profiles had data on C concentrations in the O horizon and mineral soil to a depth of 100 cm. Nitrogen concentrations (determined by the Kjeldahl method) were available for 83 profiles allowing the calculation of total N pool to a 100-cm depth. Carbon was analyzed by dry combustion (Matejovic, 1993). Clay (%) was analyzed by the hydrometer method (Gee and Bauder, 1986), pH was measured in 0.01 M CaCl₂ (soil/extract 1:2.5), and available P extracted with 0.1 M H₂SO₄ for 2 h (Murphy and Riley, 1965). When analyzing organic C, carbonate C may constitute a problem, as combustion methods do not discriminate between inorganic and organic C. This problem has either resulted in the exclusion of carbonate containing horizons from analysis, or an overestimation of C. However, only five Alfisols and one Inceptisol included in this study contained carbonates (Calcium Carbonate in glacial till developed on limestone), and the very low C concentrations measured do not indicate carbonate C interference.

Soil profiles were classified to taxonomic order level according to *Keys to Soil Taxonomy*, using mainly the fourth edition (Soil Survey Staff 1992) but also earlier editions. Thirty-four profiles were classified as Spodosols, 31 Entisols, 23 Inceptisols, 16 Alfisols, and two Mollisols, which were grouped together for parameter estimation (Table 1).

### Calculations: Soil Bulk Density, Carbon, and Nitrogen

Data on soil bulk density were available for 53 of the soil profiles. Carbon and N pools were calculated by horizon using concentration, horizon depth, and bulk density, and volumes were summed to a depth of 100 cm to express soil C and N contents in kilogram per square meter. Bulk densities ($D_b$) for remaining profiles were calculated from models specifically developed for this paper by the authors. For this purpose, data on C concentration, bulk density, master horizon, and classification were supplied by L. Tau-Strand, Norway; M. Olsson, Sweden; C.J. Westman, Finland; and K. Raulund-Rasmussen, Denmark from a larger dataset of mineral forest soil horizons in four Nordic countries ($N = 844$). Plotting bulk density vs. C concentration suggested a curvilinear relationship, and hence the independent variable (C) was transformed to stabilize variances. The square-root function gave the highest-degree of explanation in the following ANOVA, in which soil order and master horizon (A, E, B, and C), were used as class variables, and C concentration as a covariate (Eq. [1]).

$$D_b = \alpha_{soilorder} + \alpha_{masterhorizon} + \sqrt{\text{carbon}} + \epsilon_i$$  

** Soil order ($P = 0.02$), master horizon ($P < 0.0001$), and C ($P < 0.0001$) were significant, but some of the groups (by soil order and master horizon) were too small to yield good parameter estimates. The data were consequently pooled in two groups to secure a fair number of observations in each group: (i) Alfisols (loamy soils, $N = 45$ soil horizons), and (ii) Spodosols, Inceptisols, Entisols, and not classified soils (sandy soil texture, $N = 799$ soil horizons); thereby distinguishing loamy sandy soils and loamy soils from sandy soils. The model was reduced to Eq. [2] and analyzed for each dataset.

$$D_b = \alpha_{masterhorizon} + \sqrt{\text{carbon}} + \epsilon_i$$  

Significant differences between master horizons were tested in Tukey-adjusted multiple comparisons using proc GLM (SAS Institute, 1997). The A, E, and B horizons in the larger dataset did not differ significantly from each other, and were consequently grouped together for parameter estimation (Table 1).

In the Alfisol data set master horizon was not significant in the ANOVA ($P = 0.87$), and the model thus reduced to Eq. [3].

$$D_b = \sqrt{\text{carbon}} + \epsilon_i$$  

The parameter estimates are presented in Table 1. The models were validated by an independent data set of 104 bulk density determinations in Danish forest soils (Vesterdal and Jørgensen, unpublished data, 1999). In this data set, the residuals (observed − predicted bulk densities) had a normal distribution with a mean of 0.03 g cm⁻³ and a standard deviation of 0.18 g cm⁻³. Out of a total of 106 O horizons used in calculation of O horizon: mineral soil C ratios (Table 2), nine had mass determinations based on areal sampling using 25 by 25 cm frames, and 83 were assigned a bulk density based on a study by Vesterdal and Raulund-Rasmussen (1998) of forest floor bulk density in Danish forest stands. These estimates were based on 49 determinations of seven tree species in monocultures.
including spruce, beech, and oak. Values used are: 0.12 g cm$^{-3}$ for spruce, 0.06 g cm$^{-3}$ for beech, and 0.04 g cm$^{-3}$ for O horizons in oak stands. Fourteen O horizons in broadleaved stands (seven Alfisols, five Inceptisols, and two Entisols) had not been sampled at all mostly because of rapid decomposition. These profiles were given fixed C and N pools in the O horizon of 0.1 kg C m$^{-2}$ and 0.005 kg N as a LOD (limit of detection), thus allowing us to compare the relative distribution of C in the organic layer versus mineral soil. Soils with no or a very limited organic layer could thus be compared with soils with a large O horizon.

The data on C and N contents were expressed by soil order and master horizon, and assigned to the mean depth of the master horizon. Back-transformed median upper limits of the master horizons were used as reference lines to separate master horizons graphically (Fig. 2).

### Statistical Analysis

Effects of soil order (Spodosols, Alfisols, Inceptisols, and Entisols) on the total C and N pools, and C/N ratios, and contents of C and N in master horizons were analyzed in a one-way ANOVA. Multiple comparisons between soil orders were made, and probability of significant differences ($\alpha = 5\%$) was determined using the Tukey option in Proc GLM (SAS Institute, 1997). Natural log-transformation was used to achieve variance homogeneity, since the residual plot showed increasing residuals with increasing predicted values (Weisberg, 1985). Estimates and 95% confidence limits were transformed back from log-scale to linear scale. Overall population means from the ANOVA (Table 2) were adjusted by MSE/2 to correct the bias introduced when mean values of log-distributed variables are back-transformed to original scale (Parkin and Robinson, 1994). Estimates of C and N pools and C/N ratio presented in Tables 3 through 6 are back-transformed least squares means, and may be interpreted as median values on original scale. The correlation of C/N ratios with soil depth in master horizons was analyzed in a Spearman rank correlation analysis using the CORR procedure (SAS Institute, 1990).

Total C and N contents were calculated for each master soil horizon for analyses of C and N relationship to depth and genetic soil horizons. Carbon/N ratios were only calculated following A horizons and C horizons. The lowest C/N ratios were found in the B horizons.

The concentrations of C and N decreased downward to correct the bias introduced when mean values of log-distributed variables are back-transformed to original scale (Parkin and Robinson, 1994). Estimates of C and N pools and C/N ratio presented in Tables 3 through 6 are back-transformed least squares means, and may be interpreted as median values on original scale. The correlation of C/N ratios with soil depth in master horizons was analyzed in a Spearman rank correlation analysis using the CORR procedure (SAS Institute, 1990).

### RESULTS

The mean content of total C in the whole profile for all soils (O horizon + 0–100 cm) was 12.5 kg m$^{-2}$; profile values ranged from 2.9 to 29.6 kg m$^{-2}$ (Table 2). The corresponding contents of N in the soils were 0.61 kg m$^{-2}$, and the range of observations was from 0.28 to 1.46 kg m$^{-2}$. The average C/N ratio was 22.0.

The total soil C content (O-horizon + 0–100 cm) for the Spodosols was significantly greater ($P < 0.0001$) than in all other soil orders (Table 3); Alfisols had the least. In contrast, the highest N contents occurred in the Alfisols, and the lowest in the Spodosols, other orders were not significantly different. The Spodosol C/N ratio was the greatest; the Alfisol C/N ratio was the least.

The concentrations of C and N decreased downward in the profile from the O horizons (Table 4). The highest C and N concentrations were in the O horizons, whereas the lowest concentrations were found in the C horizons. Among the mineral soil master horizons, A horizons contained the largest concentrations of C and N (Table 4). The E and B master horizons (excluding Bh horizons) differed significantly in C concentration, while the N concentrations were not significantly different. The highest C/N ratios were found in the O and E horizons, followed by A horizons and C horizons. The lowest C/N ratios were found in the B horizons.

The concentrations of C in the B master horizons varied considerably; being highest in the horizons containing illuvial humus complexes; Bh and Bhs, and lowest in the Bt horizons (Table 4). The N concentrations in the five types of B horizons followed a different pattern. Again the highest concentrations were in the
Fig. 2. Depth distribution of soil organic C, N, and C/N ratio. Each master horizon was analyzed in a separate ANOVA. Error bars are 95% confidence limits of the least square mean (1.96SEM) back-transformed to original scale. Identical lower case letters indicate that master horizons in different soil orders are not significantly different at the 95% probability level. Estimates represent group medians on original scale (Parkin and Robinson, 1994).

Table 3. Carbon and N pools, and C/N ratio in O horizon 0–100 cm mineral soil (kg m⁻²). Back-transformed least squares estimates and 95% confidence limits (CL) of individual least squares means. Back-transformed group estimates represent medians on original scale (Parkin and Robinson, 1994). Identical lower case letters indicate that means are not significantly different at the 95% probability level (Tukey adjustment for multiple comparisons).

<table>
<thead>
<tr>
<th>Soil order</th>
<th>n</th>
<th>C kg m⁻²</th>
<th>CL 95%</th>
<th>n</th>
<th>N kg m⁻²</th>
<th>CL 95%</th>
<th>C/N ratio</th>
<th>CL 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spodosol</td>
<td>34</td>
<td>14.6a</td>
<td>13.1–16.4</td>
<td>28</td>
<td>0.51b</td>
<td>0.46–0.58</td>
<td>28a</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Alfisol</td>
<td>18</td>
<td>8.8c</td>
<td>7.6–10.3</td>
<td>14</td>
<td>0.75a</td>
<td>0.63–0.88</td>
<td>12c</td>
<td>10–14</td>
</tr>
<tr>
<td>Inceptisol</td>
<td>23</td>
<td>10.8bc</td>
<td>9.4–12.4</td>
<td>20</td>
<td>0.60ab</td>
<td>0.52–0.69</td>
<td>19b</td>
<td>16–21</td>
</tr>
<tr>
<td>Entisol</td>
<td>31</td>
<td>11.9b</td>
<td>10.5–13.4</td>
<td>21</td>
<td>0.57ab</td>
<td>0.49–0.65</td>
<td>23ab</td>
<td>20–26</td>
</tr>
</tbody>
</table>

Bh and Bhs horizons, whereas the Bs, Bw, and Bt were all similar.

The distribution of C and N between the O horizons and the mineral soil (C_O-org/C_0–100 and N_O-org/N_0–100) showed that Alfisols contained significantly lower amounts of C and N in the O horizon (Fig 2). The greatest C and N content in the O horizon were in the Spodosols (approximately 0.3), although only for total N was significantly different from other soil orders.

The vertical distribution of C and N content with depth and master horizon is shown in Fig. 2. Horizontal lines representing the mean upper limit of the master horizon separate the horizons. Spodosols contained the most C in the O horizons and in the B horizon compared
with other soil orders ($P < 0.0001$). Nitrogen contents in A horizons were significantly higher in Alfisols than in Spodosols and Entisols. Alfisols also had lower C/N ratios than Spodosols in both A and B horizons; Inceptisols and Entisols were intermediate, but significantly different from both Alfisols and Spodosols. Carbon/N ratios generally declined with the depth of the master horizon (Spearman rank correlation $r = -0.26$, $P = 0.0001$). Analyzed by soil order, the correlations were $-0.06^{38}$ for Spodosols, $-0.54^{* * *}$ for Alfisols, $-0.39^{* * *}$ for Inceptisols, and $-0.25^{* *}$ for Entisols (Fig. 2). Even though the overall trend was not significant, Spodosols had lower C/N ratios in A versus C horizons ($P = 0.05$). The negative correlation was because of higher C/N ratios in O horizon than B horizons in Alfisols ($P = 0.003$), and in Entisols ($P = 0.001$).

The soil clay content (%) ranged from 0 to 31% of the mineral soil. Clay was negatively correlated with O horizon C and N contents ($P < 0.001$), C/N in the O horizons ($P < 0.001$), and C/N ratio in the mineral soil ($P < 0.001$) (Table 6); and was positively correlated with N in the mineral soil ($P < 0.001$). Maximum mineral soil pH within the 100-cm soil depth was negatively correlated with C and N contents in the O horizons ($P < 0.05$), and the C/N ratio of mineral soils ($P < 0.05$), but positively with N content in the mineral soil ($P < 0.01$). Total P content of the 50- to 100-cm depth was negatively correlated with O horizon C ($P < 0.001$), N ($P < 0.01$), and C/N ratio ($P < 0.01$). Phosphorus content was negatively correlated with mineral soil C ($P < 0.01$) and was positively correlated with mineral soil N ($P < 0.05$) (Table 6).

**DISCUSSION**

Soil C and N pools are affected by climate (Post et al., 1982). The narrow climate range in our data allows studying the soil gradient in an udic mesic (i.e., temperate humid) climate, with probably minimal macroclimatic influence. The C contents in Danish forest soils (average of 12.5 kg C m$^{-2}$) are higher than the median soil C content in cool temperate moist forest of 10.1 kg C m$^{-2}$ reported by Post et al. (1982). However, global estimates exclude the litter layer. The value reported by Post et al. corresponds well to the estimated average for the 0- to 100-cm soil depth of 9.7 kg C m$^{-2}$ (Table 1). Soil C ranges reported by other authors for temperate humid climates include both higher and lower values, for example, 4.0 to 11.9 kg m$^{-2}$ in Finland (Westman et al., 1994), and 1.9 to 20.7 kg C m$^{-2}$ in a regional study in the USA (Franzmeier et al., 1985). Grigal and Ohman (1992) compared five coniferous and broadleaved forest types in the Lake States of the USA and found O-horizon C in the range from $1$ to 4 kg C m$^{-2}$, being highest for the conifer species. Mineral soil C to 1 m ranged from 7 to 15 kg C m$^{-2}$. Our estimate of Danish litter layers (3.9 kg C m$^{-2}$) is comparable with the estimates for conifers in the study of Grigal and Ohman (1992), and reflects the tree species distribution in our data with conifers growing at more than 75% of the sites on all soil orders, except Alfisols (only 28% conifers). The estimate for Alfisol O-horizons reflects the tree species distribution on these soils. O-horizon mass in both beech and spruce stands is negatively correlated with soil fertility, but spruce stands accumulate more C than beech irrespective of soil type (Vesterdal and Raulund-Rasmussen, 1998).

Estimates of total N through the soil profile exist in the literature, but estimates of soil N including N in both O horizon and mineral soil to depth are rare. Carter et al. (1998) found 0.36 to 1.05 kg N m$^{-2}$ in Canadian agricultural soils. Compared with these values, the Danish forest soils had intermediate N contents. Zinke and Stangeberger (2000) reported median values of 0.61 kg N m$^{-2}$ to a 1-m depth in dense conifer forest, and 0.27 kg N m$^{-2}$ in low density forest on the lower western slopes of the Sierra Nevada, CA. It was not stated explicitly whether those values included the O-horizon. As-

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**Table 4. Concentrations of C and N in master horizons. Bh horizons are excluded from other B horizons, B (-Bh), in the comparison of master horizons. Back-transformed group estimates represent medians on original scale (Parkin and Robinson, 1994). Identical lower case letters indicate that means are not significantly different at the 95% probability level (Tukey adjustment for multiple comparisons).**

<table>
<thead>
<tr>
<th>Master horizons</th>
<th>n</th>
<th>C</th>
<th>CL 95%</th>
<th>n</th>
<th>N</th>
<th>CL 95%</th>
<th>n</th>
<th>C/N</th>
<th>CL 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>117</td>
<td>348a</td>
<td>298–406</td>
<td>122</td>
<td>12.6a</td>
<td>11.0–14.3</td>
<td>116</td>
<td>27a</td>
<td>24–30</td>
</tr>
<tr>
<td>A</td>
<td>185</td>
<td>21.7b</td>
<td>19.2–24.5</td>
<td>171</td>
<td>3.01b</td>
<td>2.91–1.13</td>
<td>171</td>
<td>21b</td>
<td>19–23</td>
</tr>
<tr>
<td>E</td>
<td>71</td>
<td>7.3c</td>
<td>5.9–8.8</td>
<td>57</td>
<td>0.35c</td>
<td>0.29–0.42</td>
<td>56</td>
<td>24a</td>
<td>21–28</td>
</tr>
<tr>
<td>B (-Bh)</td>
<td>282</td>
<td>4.5d</td>
<td>4.1–4.9</td>
<td>225</td>
<td>0.29c</td>
<td>0.27–0.32</td>
<td>218</td>
<td>18b</td>
<td>17–20</td>
</tr>
<tr>
<td>C</td>
<td>132</td>
<td>1.1e</td>
<td>1.0–1.3</td>
<td>81</td>
<td>0.08d</td>
<td>0.07–0.10</td>
<td>56</td>
<td>20ab</td>
<td>18–24</td>
</tr>
</tbody>
</table>

**Table 5. CO/C100 and NO/N100 (O horizon C and N to mineral soil horizon C and N 0–100 cm), and 95% confidence limits (CL) of least squares means. Back-transformed group estimates represent medians on original scale (Parkin and Robinson, 1994). Identical lower case letters indicate that means are not significantly different (Tukey adjustment for multiple comparisons).**

<table>
<thead>
<tr>
<th>Soil order</th>
<th>n</th>
<th>CO/C100</th>
<th>CL 95%</th>
<th>n</th>
<th>NO/N100</th>
<th>CL 95%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spodosol</td>
<td>34</td>
<td>0.31a</td>
<td>0.20–0.48</td>
<td>28</td>
<td>0.30a</td>
<td>0.18–0.49</td>
</tr>
<tr>
<td>Alfisols</td>
<td>18</td>
<td>0.04b</td>
<td>0.02–0.06</td>
<td>14</td>
<td>0.02c</td>
<td>0.01–0.03</td>
</tr>
<tr>
<td>Inceptisol</td>
<td>23</td>
<td>0.14a</td>
<td>0.08–0.24</td>
<td>20</td>
<td>0.10b</td>
<td>0.05–0.17</td>
</tr>
<tr>
<td>Entisol</td>
<td>31</td>
<td>0.28a</td>
<td>0.18–0.44</td>
<td>21</td>
<td>0.17ab</td>
<td>0.10–0.30</td>
</tr>
</tbody>
</table>
suming exclusion of the O-horizon these values bracket our estimate of 0.5 kg N m\(^{-2}\) for mineral soil to a 1-m depth (Table 2). Batjes (1996) calculated soil C and N storage in 1 m of mineral soil using worldwide databases, and found rather high soil N contents, for example, 1.39 kg N m\(^{-2}\) for Podzols (Spodosols), 1.03 kg N m\(^{-2}\) for Luvisols (Alfisols), and 0.52 kg N m\(^{-2}\) in Arenosols (Entisols). Other soil orders also had higher mean values for soil N than our data. However, comparison is not straightforward for three reasons: (i) the means reported in Batjes (1996) are probably skewed to the right (Zinke and Stangenberger, 2000), and (ii) the distribution of land uses was not reported, but agricultural soils are probably a prevalent land use in the data, and (iii) the global data reflect the distribution of global climate zones, whereas our estimates pertain to a cool, humid temperate climate. Eriksson and Rosén (1994) estimated total soil N to a 95-cm soil depth (including O-horizon) to be 0.5 to 0.65 kg N m\(^{-2}\) in a tree species trial with conifers in southwestern Sweden. The climate is similar to the Danish climate, and the contents of soil N appear quite similar.

The only deviation from the general pattern of gradually decreasing C and N concentrations with depth occurred in soils with a spodic horizon (Bh, Bhs). The pattern in C and N concentration was O > A > E < Bh, Bhs > C (Table 4). The C concentrations of spodic Bh and Bhs horizons (Table 4) indicate that the podzolization process is responsible for the accumulation of C, and expressed by contents (kg m\(^{-2}\)) this is also illustrated in Fig. 2. Accordingly, our analysis showed that podzolized soils contain more C than the other soil orders. Entisol profiles, containing large quantities of C, usually had a horizon with spodic properties, which, because of insufficient thickness, did not meet the formal requirements of a spodic horizon (Soil Survey Staff, 1992). Normally, soils that do not meet the requirements for inclusion in a major soil order end up in the Inceptisol order. However, the widespread Danish coarse-sandy textured soils do not comply with the requirements for a cambic horizon; and they lack the dark color required for an umbric epipedon, since the upper epipedon is often dominated by albic material. Therefore, many podzolized sandy soils of Denmark are classified as Entisols, unless they possess a spodic placic horizon in the Bh or Bhs horizon. Westman et al. (1994) also attributed the podzolization process per se to the immobilization of significant amounts of C (4.0–11.9 kg m\(^{-2}\)) in a study of forest soils in Finland. The cooler climatic conditions and soil ages of >6000 yr in Finland are probably the reasons for higher Spodosol C pools of this study. Hence, in Spodosols and Spodic Udipsamments, the quantity of organic C is probably predictable from information on soil order and suborder. Other studies on Spodosol C pools found C stores of 10.4 kg C m\(^{-2}\) (Stone et al., 1993), 17.4 to 29.8 kg C m\(^{-2}\) (Es- waran et al., 1993), and 9.0 to 11.8 kg C m\(^{-2}\) (Martel and Deshenges, 1976). Gregorich et al. (1995) also found more C in podzolic soils (Spodosols) than in luvisolic soils (Alfisols). The differences are because of variations in the soil forming factors, not least being soil age. Extended periods of time allows for creation of deep spodic horizons. Climate and hence primary production play a major role too.

In contrast to C stores, N stores in this study were highest in Alfisols. Alfisols are generally base rich and have characteristically high rates of decomposition because of high litter quality, that is, high nutrient concentration content (Vesterdal, 1999), and a more favorable environment for decomposers, for example, more stable soil moisture content because of a higher water storage capacity. The Spodosols possess the lowest N stores because of the lower quality of litter (Vesterdal, 1999), and in combination with the huge quantities of C, it explains the higher C/N ratios of this soil order. The ratios \(C_{O-hor}/C_{0-100}\) and \(N_{O-hor}/N_{0-100}\) demonstrate the importance of the O horizons as forest ecosystem C and N pools (Table 5). In Spodosols and Entisols, the ratios for C were 0.31 and 0.28, respectively, and for N the ratios were 0.30 and 0.17. The variation in the C and N contents of O horizons was because of variation in thickness and mineral matter content of the O horizon. The O horizon contained from <1 to 150% (data not shown) of total soil C and N present in depth 0 to 100 cm. Grigal and Ohmann (1992) found 55% of total ecosystem C (including the living biomass) in the mineral soil, and 9% in the forest floor, that is, a \(C_{O-hor}/C_{0-100}\) ratio of 0.16, which is similar to the Inceptisols in our study. McFee and Stone (1965) found 43% of the N content and 38% of the organic matter content of the total system, including the standing crop, in the O horizon of forest soils. These results show that O horizons should be included in any estimation on soil C and N pools, though this compartment is often underestimated or ignored in pedological studies (Eswaran et al., 1995).

The narrowing C/N ratio downwards in the profile from O to A and B horizons (excluding Bh horizons) may be because of the decomposition stage and age of humus in horizons (Lal et al., 1995). However, E and C horizon C/N ratios were not significantly different.
from O horizon C/N ratios. Recently shed litter has a high C/N ratio, this ratio decreases during decomposition. As the age of organic matter increases with soil depth (Lal et al., 1995), the C/N ratio consequently decreases. The decreasing C/N ratios with depth and age of organic matter may be attributed to microbial immobilization of N and loss of C through respiration (Aber and Melillo, 1980; Staaf and Berg, 1982).

The inverse relationship between clay content and C content, N content, and C/N ratio in the O horizons found in this study is a result of the O horizons associated with Spodosols. Interestingly, the total amount of C (O horizon + 0–100 cm) is also negatively related to clay content. This suggests that fertile Alfisols with humus rich A horizons are surpassed by the sandy nutrient-poor Spodosols in terms of C sequestration. Spodosols have two C sinks; the O horizon and the Bh/Bhs horizon. These results are in contradiction to the findings of Grigal and Ohmann (1992), who concluded that C content was positively related to clay content, probably by its influence on soil moisture and fertility. Several other studies suggested that soil C and soil clay is positively related to clay content (Oades, 1988; Burke et al., 1989), or not related (Carter et al., 1998).

The same sort of relationship is demonstrated by using the extractable P content (g m⁻²) in depth 50 to 100 cm, as an indicator of site fertility. The C and N contents, the C/N ratio of the O horizons, and the total C content of the soil profile are negatively related to P content. On the other hand, the fertile soils contain the highest amounts of N as demonstrated by the weakly positive relationship between mineral soil N content and P content. The chain of mechanisms behind this may be that fertile soils have high productivity, but also high decomposition rates, resulting in low C contents. However, the fertile sites have relatively high N contents, possibly because humus with low C/N ratios is protected in organo-mineral complexes as suggested by Christensen (2000).

A concern in many soil C and N studies that rely on data from previously conducted studies is that data may contain errors because of differences in the sampling and analytical methods of the original studies (Eswaran et al., 1995). Estimations of C and N pools in this study were potentially compromised by measurement errors in bulk density, soil volume calculations, C and N determinations, and stoniness of soils. A lack of bulk density data is a common problem for estimation of global soil C pools (Carter et al., 1998), and our predictions of missing bulk densities may add to the error. Murillo (1994) estimated the compounded error of soil profile organic C estimates to be 30%, which is a realistic error estimate for our data. The sources of error might introduce a bias, when comparing soil C and N content among studies in the literature where different methodologies have been applied. However, none of these sources of error introduce a bias among soil orders, and with a high number of profiles the error is diminished, thus justifying the use of pedological soil databases for ecological purposes. However, tree species and soil order are confounded. This affects the O-horizon estimates, but it nevertheless reflects the distribution of tree species in Denmark.

When interpreting data from natural systems, the multidimensional features of these systems should be taken into account. Grigal and Ohmann (1992) used a multiple regression technique; 65% of the variation in total forest C was attributed to forest type, stand age, available water capacity, actual evapotranspiration (AET), and soil clay content. Our results suggest that horizon designation, horizon thickness, and soil order are predictors of total soil C and N content; all based on pedology. Percentage of clay, although correlated to C content, is not a predictor of soil development, or the degree of podzolization on sandy soils. The P content of the subsoil (the 50- to 100-cm stratum) seemed to be a suitable indicator, but such data are not generally available in soil surveys. Soil pH did not prove an adequate variable for prediction of soil C and N content. Our study clearly suggests that soil order may predict the levels of C and N. At least a distinction in C and N content between the two major Danish soil orders, Alfisols and Spodosols, is possible under the given climatic conditions. For soils possessing spodic properties, sound estimates on C and N content should also be possible.

If soil C sequestration becomes a primary goal of forest management, afforestation in Denmark should take place on Spodosols or soils with spodic properties. Podzolization mechanisms favor accumulation of large O horizons and the formation of humus-rich spodic horizons. This was also proposed by Cannell and Milne (1995) who concluded that the equilibrium storage of C is greatest when litter decompose slowly and a large fraction is transferred to recalcitrant soil organic matter pools. Our study suggests that C storage in Danish forest soils is most likely because of impeded decomposition in nutrient poor soils, and not driven by high productivity at nutrient-rich soils.

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