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The carbon pools in a Danish semi-natural forest

Lars Vesterdal and Morten Christensen


There is currently little knowledge of the potential for carbon (C) storage in temperate beech forests. Beech forest reserves subject to little or no human intervention may serve as benchmark forests to determine this potential. We estimated the C stock and the distribution of the C stock between tree biomass, dead wood, forest floor and mineral soil in a part of Suserup Skov where all phases of the natural forest cycle were represented. The total C stock of the forest was 382 Mg ha⁻¹. The largest proportion of C (225 Mg ha⁻¹) was in woody biomass > 3 cm. Dead wood, which is a unique pool of C in such a forest reserve, contributed 21 Mg ha⁻¹ or 6% to the total C stock, whereas forest floor C stocks including smaller woody debris contributed only 4.5 Mg ha⁻¹ or approximately 1% to the total C stock. The forest floor C content was relatively insignificant in this forest as rates of decomposition are high, but the mineral soil contained the second-largest amount of C to 1 m depth (132 Mg ha⁻¹). The total C stock of Suserup Skov is considerably higher than in mature managed beech forests. This suggests that there is a potential for increasing C stocks in conventionally managed beech-dominated forests of the region, possibly by adoption of natural forest structures and focused management of dead wood in the managed beech forests.

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Forests store carbon (C) in vegetation, dead wood, forest floors and mineral soils. The Kyoto Protocol has in particular raised the question to which extent we are able to increase the C stock of forests by changing the management. The most recent estimate of the C stock in woody biomass of Danish forests was 57 Mg C ha⁻¹ (Larsen and Johansen 2002). As the main parts of Danish forests are regenerated by clear-cutting, this figure is an average covering clear-cut areas, young stands and mature stands. In managed forests, significant C pools are also found in soils including the forest floor that blankets the mineral soil, but dead wood amounts are very limited (Green and Peterken 1997) and thus contribute little to the total C stock.

During the last decades, forestry in several European countries has initiated a change in management of deciduous forests toward nature-based or continuous cover forestry (Pommerening and Murphy 2004). This management form is inspired by natural forests where disturbance occurs down to the single tree level, i.e. there is almost continuous crown cover over time. There is currently little knowledge of the influence of this change in management on C stocks. Possibly, more C could be stored as a result of this change in management, as the traditional clearcutting system is known to have low C stocks in the regeneration period with no canopy cover (Liski et al. 2001). An important characteristic in nature-based forestry is the more con-
tinuous canopy cover or at least the smaller and less long-lasting openings in the forest canopy. This means that in the long-term there is a higher average biomass C stock per ha in such forests compared to traditional clear-cutting/replanting systems. Nature-based forest management possibly also preserves more C in soils compared to the clear-cutting system, where the soil C stock may decrease in the period following clear-cutting and replanting (Covington 1981, Heinsdorf 2002, Peltoniemi et al. 2004). Soils may also be prone to fewer disturbances, thereby conserving larger C stocks than in traditionally managed forests.

Compared to traditionally managed forests, reserves in natural forest are not exploited with respect to wood. A greater amount of biomass C is therefore left on site, which also sustains a larger pool of C in dead wood (Green and Peterken 1997, Fridman and Walheim 2000, Hahn and Christensen 2004). In Pacific Northwest, Harmon et al. (1990) reported that conversion of old-growth forests to plantations would result in a significant release of C to the atmosphere due to lower C stocks in plantation forests. Fleming and Freedman (1998) similarly found that a landscape managed as a shifting mosaic of plantations on a 60-yr rotation would store only ca 22% as much aboveground C as a landscape covered in old-growth natural forests with gap-phase disturbance dynamics. They attributed this to lower biomass levels and to the paucity of snags and coarse woody debris in the managed forests. In a meta-analysis of effects of land-use change on soil C, Guo and Gifford (2002) found indications that the soil C stock may be reduced by 13% following conversion from native forests to plantation forestry. In managed forests with a mixture of even-aged stands of different age classes, average total C stocks are usually lower, as the biomass C stock is obviously at a low level in recently clearcut or reforested areas. For forests in the German state Rheinland-Pfalz, Schöne and Schulte (1999) reported ecosystem C stocks for different major tree species from 197 to 236 Mg ha⁻¹ with the largest part of the C stock in soils (ca 60%).

In order to address the possible effect on C storage of conversion to nature-based management, it is relevant to know the potential for C storage in different European forest ecosystems when there is no or little human intervention. Hooker and Compton (2003) recently stressed the need for such benchmark old-growth forests to determine potential biomass recovery after abandonment. The few small remaining areas of semi-natural or unmanaged natural forest types may serve as such benchmark forests with respect to various ecosystem properties. The C stock of a forest in structural steady state, i.e. a forest comprising areas of all phases in the forest cycle (Watt 1947) could serve as a benchmark of potential C stocks when there is no management involved.

The objective of this study was to provide such a reference for C stocks in beech-dominated Danish forests and to assess the partitioning of C in different components of the forest ecosystem. Suserup Skov represents the cool-temperate nemoral beech-dominated forest type. As such it may provide valuable information on potential C stocks in beech-dominated forests of the region. Carbon pools in living woody biomass, dead wood, and soils were estimated in a part of Suserup Skov, which was previously reported to be within the structural steady state characteristic of natural forests (Emborg et al. 2000).

Materials and methods

Suserup Skov (19.2 ha), located on central Zealand (55°22'N, 11°34'E), is one of the few semi-natural forests left in Denmark. Carbon stocks were estimated for a part of Suserup Skov (10.7 ha) reported to have the longest history as non-intervention forest and thus also with the structural features of a natural forest (Emborg et al. 2000). It is a mixed deciduous forest with a stand basal area of 40 m² ha⁻¹. European beech Fagus sylvatica and common ash Fraxinus excelsior dominate (56.1 and 28.1% of basal area, respectively), but also several pedunculate oak Quercus robur and wych elm Ulmus glabra are present. The soil is nutrient-rich and developed from glacial deposits. The C horizon is calcareous and contains ca 20% clay. Smaller patches of sandy till occur within the dominating loamy till material (Veje and Emborg 1996). The soil was classified as an Inceptic Hapludalf according to Anon. (1992). For more information about the forest in general and the studied part, see Emborg et al. (1996) and Heilmann-Clausen et al. (2007).

The climate is cool-temperate with a mean annual temperature of 8.1°C and a mean annual precipitation of ca 650 mm, the majority of which falls in late summer and autumn.

Volume and C content of woody biomass

The volume of living trees was measured May–August 2002. All trees > 30 cm DBH (diameter at breast height, 1.3 m) were measured within the 10.7 ha plot. Small trees between 3 and 30 cm DBH were measured in three representative 1-ha sample plots. Tree heights were estimated using species-specific diameter-height regressions from Suserup Skov (Emborg et al. 1996). Volume of merchantable biomass was calculated by diameter class based on basal area, height and a form factor derived from the Danish standard volume functions for beech (Madsen 1987; for details see Emborg et al. 1996). For broadleaved trees, merchantable wood includes the stem and branches. Carbon contents of total (above- and belowground) woody biomass was calculated by the methods used in Danish National Inventory Reports under United Nations Framework Convention on Climate Change (Illerup et al. 2005). These methods include tree species specific basic wood densities (in average 0.56 t dw m⁻³ fresh volume for
broadleaved trees), an expansion factors to estimate total below- and aboveground biomass from merchantable biomass (1.2), and wood C concentration (0.5 g C g⁻¹ dw). As no national data are available for broadleaved tree species to support development of expansion factors, the applied expansion factor is based on studies on biomass distribution in Sweden, and Belgium (Nihlgård and Lindgren 1977, Vande Walle et al. 2001). It is assumed that the distribution of tree biomass in these countries is comparable to biomass distribution in Denmark.

**Volume and C content of dead wood**

The volume of dead wood was measured December 2001 using line-intersect sampling (Warren and Olsen 1964, Kirby et al. 1998). A total of fifteen 50 m transects were laid out from random starting points and in random directions. The number of fallen dead wood pieces (>5 cm diameter) intersecting the line was counted. Diameter was measured in cm where dead wood pieces intersected the line, and the species was identified. Dead wood intersections were assigned to diameter classes and the mean cross-sectional area for that class was calculated. The total volume of fallen dead wood (m³ ha⁻¹) in each diameter class then equals the length for that class multiplied with the cross-sectional area, i.e.

\[
V = nd^2 \pi^2 10^3/8t
\]

where \( V \) is the total volume of fallen dead wood of diameter class \( d \) (the diameter being measured at the intersect with the transect line), \( n \) is the number of intersections for dead wood pieces of diameter \( d \), and \( t \) is total length of transects in metres (Kirby et al. 1998). The conversion factor of 10⁶ is needed to change the results to volume (m³) per hectare rather than per m². For the forest area as a whole the volume per hectare is the sum of the volumes for each diameter class. The volume of standing dead wood (snags) was estimated from an area of 10 m width along the same transects. Snag volume was calculated from information on height and diameter.

The decay class of dead wood was determined using a key for a six-class scale (Table 1). Each piece of dead wood was assigned to a decay class by testing hardness combined with a visual estimation of outline and bark.

Sampling of dead wood for C analysis was done in September 2000. Wood samples were taken from the surface towards the centre of the logs using drilling equipment. For all downed logs six samples were taken from different angles, except for the down facing part. From snags higher than 2 m, six samples were drilled from six different directions and in different heights ranging from 0.5 to 1.5 m above the ground. All samples were ground and samples from each log and snag were pooled into a composite sample. Carbon concentration was determined by the Dumas method (Matejovic 1993) using a Leco CNS-2000 analyzer. Wood composite samples (100–200 mg) were oxidized to CO₂ at 1350°C. The amount of CO₂ was measured using an infrared detection method.

For estimation of basic wood density of dead wood, one piece of representative wood (ca 3 x 3 x 3 cm) was taken from each log and snag. The collection was done during rather moist winter conditions (February 2002), which in-

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**Table 1. Characteristics of the six decay classes used for dead wood.**

<table>
<thead>
<tr>
<th>Decay class</th>
<th>Bark</th>
<th>Twigs and branches</th>
<th>Softness</th>
<th>Surface</th>
<th>Shape</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Intact or missing only in small patches, &gt; 50%</td>
<td>Present</td>
<td>Hard or knife penetrates 1–2 mm</td>
<td>Covered by bark, outline intact</td>
<td>Circle</td>
</tr>
<tr>
<td>2</td>
<td>Missing or &lt; 50%</td>
<td>Only branches &gt;3 cm present</td>
<td>Hard or knife penetrates &lt; 1 cm</td>
<td>Smooth, outline intact</td>
<td>Circle</td>
</tr>
<tr>
<td>3</td>
<td>Missing</td>
<td>Missing</td>
<td>Begin to be soft, knife penetrates 1–5 cm</td>
<td>Smooth or crevices present, outline intact</td>
<td>Circle</td>
</tr>
<tr>
<td>4</td>
<td>Missing</td>
<td>Missing</td>
<td>Soft, knife penetrates &gt; 5 cm</td>
<td>Large crevices, small pieces missing, outline intact</td>
<td>Circle or elliptic</td>
</tr>
<tr>
<td>5</td>
<td>Missing</td>
<td>Missing</td>
<td>Soft, knife penetrates &gt; 5 cm</td>
<td>Large pieces missing, outline partly deformed</td>
<td>Flat elliptic</td>
</tr>
<tr>
<td>6</td>
<td>Missing</td>
<td>Missing</td>
<td>Soft, partly reduced to mould, only core of wood</td>
<td>Outline hard to define</td>
<td>Flat elliptic – covered by soil</td>
</tr>
</tbody>
</table>
icates that wood moisture was close to the maximum "natural" level at sampling. Volumes were measured on wet samples (after at least 2 h in water) in water and dry weights were measured after drying at 105°C for at least 24 h until the weight was stable.

Carbon content of dead wood was finally calculated by multiplying volume, density and C concentration for each diameter class. The reported C content of dead wood for the forest is the sum of C contents of each diameter class.

**Forest floor C content**

Forest floors were defined as the organic layer consisting of shed leaves, twigs and branches above the mineral soil, i.e. equivalent to O horizons. Forest floors were mull-like and mainly consisted of recently shed leaves and twigs, i.e. there was no distinct humus layer. Forest floors were sampled on an area basis by using a 25 x 25 cm wooden frame. Sampling was done carefully in order to avoid contamination with mineral material as far as possible. Six subsamples were randomly collected in March 2000 around the soil pit (see below). Subsamples were dried at 60°C, and the material was weighed (+1 g). The six subsamples were ground and pooled to one sample for C analysis by dry combustion (Dumas method) in a Leco CNS-2000 as described for dead wood. Forest floor C stocks were estimated by multiplying C concentrations by dry mass per ha.

**Mineral soil C content**

Data from four soil pits were included in the study. One soil pit was dug in March 2000 at a plateau in the northeastern part of the forest area. The soil pit was described and subsequently soil was sampled by genetic horizon for C analysis and bulk density determination (2 samples). Soil samples for C analysis were air dried and sieved (2 mm). Samples were then ground in an agate mortar and analyzed for total C by dry combustion as for dead wood and forest floors. The two samples per horizon for bulk density determination were sieved (2 mm) and dried to constant weight at 105°C.

Data on three other soil pits within the studied area of Suserup Skov were reported by Vejre and Emborg (1996). Information on bulk density was not available in this study, and bulk densities by genetic horizon were thus estimated using a pedotransfer function based on similar Danish soil types (Alfisols) (Callesen et al. 2003, Vejre et al. 2003).

Of the four soil profiles, two represented the undulating northern part of the forest and the other two represented the more level area close to the lake (see map in Heilmann-Clausen et al. 2007).

For all four soil profiles, mineral soil C content for the fraction > 2 mm were neglected (McNabb et al. 1986), and soil organic C (SOC) stocks in [Mg ha⁻¹] were estimated by genetic horizon i via

$$SOC_i = \rho_i (1 - (\delta_{2mm}/100)) d_i C_i$$

where $\rho_i$ is the bulk density of the < 2 mm fraction in g cm⁻³, $\delta_{2mm}$ is the relative volume of the fraction > 2 mm (%), $d_i$ denotes the thickness of layer i in cm, and C_i denotes the C concentration of layer i. Carbon stocks of horizons were then summed to a depth of 1 m. Information on stone contents were not available and mineral soil C stocks may therefore be slightly overestimated in some of the four soil profiles.

**Results**

### Biomass C content

The merchantable woody biomass amounted 670 m³ ha⁻¹, and by use of the various to conversion factors the C stock of both above- and belowground woody biomass was estimated at 225 Mg C ha⁻¹ (Table 2). Beech contributed most to the biomass C stock followed by ash and oak as a direct consequence of the species distribution of mer-

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**Table 2.** The distribution of biomass C among the most dominant tree species. Merchantable wood is stem and branch wood whereas biomass C includes both above-and belowground C.

<table>
<thead>
<tr>
<th>Species</th>
<th>Merchantable wood (m³ ha⁻¹)</th>
<th>C stock (Mg ha⁻¹)</th>
<th>Relative C distribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fagus sylvatica</em></td>
<td>429</td>
<td>144</td>
<td>64</td>
</tr>
<tr>
<td><em>Fraxinus excelsior</em></td>
<td>105</td>
<td>35</td>
<td>16</td>
</tr>
<tr>
<td><em>Quercus robur</em></td>
<td>99</td>
<td>34</td>
<td>15</td>
</tr>
<tr>
<td><em>Ulmus glabra</em></td>
<td>22</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td><em>Tilia platyphyllos</em></td>
<td>10</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Other species</td>
<td>5</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>670</strong></td>
<td><strong>225</strong></td>
<td><strong>100</strong></td>
</tr>
</tbody>
</table>
Table 3. Measured variables and calculated C stocks for dead wood decay classes.

<table>
<thead>
<tr>
<th>Decay class</th>
<th>Volume (m³ ha⁻¹)</th>
<th>Basic density (g cm⁻³)</th>
<th>C concentration (mg g⁻¹)</th>
<th>C stock (Mg ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>33.5 (20)</td>
<td>0.42</td>
<td>474</td>
<td>6.7 (32)</td>
</tr>
<tr>
<td>2</td>
<td>16.7 (10)</td>
<td>0.32</td>
<td>471</td>
<td>2.5 (12)</td>
</tr>
<tr>
<td>3</td>
<td>37.6 (22)</td>
<td>0.23</td>
<td>467</td>
<td>4.0 (20)</td>
</tr>
<tr>
<td>4</td>
<td>58.9 (35)</td>
<td>0.21</td>
<td>466</td>
<td>5.8 (28)</td>
</tr>
<tr>
<td>5</td>
<td>19.2 (12)</td>
<td>0.17</td>
<td>473</td>
<td>1.5 (7)</td>
</tr>
<tr>
<td>6</td>
<td>2.2 (1)</td>
<td>0.10</td>
<td>470</td>
<td>0.1 (&lt;1)</td>
</tr>
<tr>
<td>Total</td>
<td>168.0</td>
<td></td>
<td></td>
<td>20.5</td>
</tr>
</tbody>
</table>

Note: numbers in brackets are percentage of total.

chantable wood. The total amount of C in woody biomass is equivalent to 825 Mg CO₂ ha⁻¹.

Dead wood C content

The total volume of dead wood was 168 m³ ha⁻¹ resulting in a total C stock of dead wood of 21 Mg ha⁻¹ (Table 3). Dead wood C amounted to 9.3% of the C stock estimated for total woody biomass. The main part of the dead wood volume was beech (74%) followed by oak (21%). Decay class 4 contributed most to the total volume of dead wood (35%), whereas decay class 1 contributed most to the total C stock of dead wood (32%) (Table 3). The younger decay classes contributed relatively more to total C stock than to total volume as density of dead wood decreased with increasing age and decay class. Carbon concentration was constant across decay classes.

Forest floor and mineral soil C content

Soil C is found in both forest floor and the mineral soil. In Suserup Skov the forest floor is thin and mainly consists of litter from the last litterfall event. Decomposition is fast and only 4.5 Mg C ha⁻¹ is stored in this part of the soil profile (Fig. 1). In this forest ecosystem, the mineral soil is by far the most important soil compartment for C storage with an average C content of 132 Mg ha⁻¹. Mean values for mineral soil C content based on the four soil pits are given in Fig. 2.

The C content decreases relatively gradually which is common for nutrient-rich till soils in Denmark (Fig. 2a). Most C is located within the top 30 cm of the mineral soil, which in most cases corresponds to the A-horizon. The C concentration in 0–30 cm ranged from 16 to 23 mg g⁻¹ resulting in soil C contents of ca 70 Mg C ha⁻¹ or 53% of the C stock to 1 m (Fig. 2b). About 100 Mg C ha⁻¹ (75% of total C content) is found within the upper 50 cm of the mineral soil. Only low C contents of 6 Mg C ha⁻¹ were found for each 10 cm layer below 50 cm where C concentrations were 3.8 mg g⁻¹ on average.

Total C stock

The sum of C pools in woody biomass, dead wood, forest floor and mineral soil amounts to 382 Mg ha⁻¹ (Table 4). Woody biomass accounts for the main part of the stored C in Suserup. More than half of the total C is stored in woody biomass. Mineral soil is the second-most important ecosystem compartment with about one third of total C. Dead wood accounts for just 6% of total C and forest floors are quite insignificant for C stock assessment in this specific natural forest ecosystem.

Discussion

The C pools of Suserup Skov

The results provide an estimate of the C stock and its distribution in the nemoral beech-dominated natural forest type of eastern Denmark. The C stock reported is representative only of Suserup Skov, but nevertheless the results give an impression of the potential C stock for a semi-natural beech-dominated forest subject to structural steady state conditions (Emborg et al. 2000).

Biomass C stocks (225 Mg ha⁻¹) were relatively high in Suserup Skov. For Germany, biomass C stocks in managed 200-yr-old beech forests were reported to be around 150 Mg C ha⁻¹ (Dieter and Elsasser 2002). In a study of British semi-natural woodlands, Patenaude et al. (2003) found that two non-intervention stands dominated by ash and field maple (70–80 yr) contained only 133 and 115 Mg C ha⁻¹, respectively. The volume of living merchantable wood in Suserup (670 m³ ha⁻¹) is also high compared to most non-intervention forest reserves in northern Europe. A study of 18 reserves in north European lowland and central European submontane areas with beech dominated
Fig. 1. One of the four soil profiles excavated at Suserup. Note the deep, dark A horizon indicating a high C concentration and the shallow forest floor.

Fig. 2. (a) Carbon content in mineral soil and (b) cumulative amounts of C by each 10 cm layer down to 100 cm. Error bars are standard errors of the mean.

forest shows an average volume of 538 m³ ha⁻¹ (Christensen et al. 2005). A study of 9 forest reserves in the southern Baltic region reported an average volume of 479 m³ ha⁻¹ (Hahn and Christensen 2004). The highest wood volumes in Europe are found in montane mixed beech forest in eastern and central Europe (Hahn and Christensen 2004, Christensen et al. 2005). Forest biomass varies tremendously within Europe depending on tree species, soil type, climatic conditions and management. In Suserup Skov there is no active management and the high merchantable biomass stocks, and in turn biomass C stocks, can be attributed to the very favourable growth conditions. Beech and ash in Suserup Skov attain large heights and volumes for Danish conditions. The soil at Suserup is very rich in nutrients, and water supply on the south-facing slope is also very favourable to tree growth. The high biomass C stock in Suserup compared to C stocks in some British semi-natural forests (Patenaud et al. 2003) can also be attributed to the long period of non-intervention which has enabled trees to grow to their maximum size. In Suserup Skov, trees are also present for a longer time after they attain their maximum size compared to managed forests, where harvesting shortcuts the natural forest cycle.

Managed beech forests in Denmark contain much less C in the biomass than the beech-dominated forest at Suserup. The most recent forestry census estimated that beech stands on average contained 77 Mg C ha⁻¹ (Larsen and Johansen 2002). This is for the main part due to the shifting mosaic of stands in managed forests where large areas can have quite low biomass volumes, e.g. old stands undergoing natural regeneration or young stands with low biomass levels. Compared to managed beech forests, natural forests with small-scale gap disturbance dynamics seems to
be able to store more biomass and thus C on average over time as also reported by Harmon et al. (1990) and Fleming and Freedman (1998). Our results are in line with a British study of five semi-natural stands in a forest reserve, which suggested that managed broadleaved forests with little understory present store less C (Patenau et al. 2003). However, it is necessary to temper conclusions regarding effects of management by the fact that Suserup Skov only serves as a case study on C storage in a natural forest. Productivity is high in Suserup Skov as judged from tree height, and regeneration potential is very high. The biomass C stock of this forest would therefore also be higher than the average for Danish forests if it had the same age-class distribution as Danish beech forests. Thus, we refrain from extrapolating the C stocks of Suserup Skov to Danish beech forests in general.

Apart from the high biomass C stock, the main difference in C pools between Suserup Skov and managed Danish forests is the presence of dead wood with a diameter above 5 cm. This pool of C is virtually absent from Danish forests where very little dead wood has been left following thinning and harvesting operations. There is little information on dead wood in Danish forests, but in Belgium, Vande Walle et al. (2001) found only 0.3 and 0.8 Mg C ha\(^{-1}\) in dead wood > 5 cm diameter in a managed oak-beech and a managed ash stand, respectively. In the UK, Green and Peterken (1997) reported that dead wood volumes in managed forests were no more than 30% of the dead wood volumes in unmanaged forests and usually very much lower. It is therefore of special interest to quantify the contribution of this organic matter pool to the C stock of natural forests. The volume of dead wood in Suserup is comparable to the amounts found in other non-intervention reserves in European beech-dominated forest (Hahn and Christensen 2004, Christensen et al. 2005). Christensen et al. (2005) analysed data from 86 forest reserves and found a mean volume of 130 m\(^3\) ha\(^{-1}\). The C stock of the dead wood component at Suserup was quite similar to the amount reported (28 Mg ha\(^{-1}\)) from an unmanaged beech forest in Hungary (Ódor and Standovár 2003), but much higher than the amount (2 Mg C ha\(^{-1}\)) reported from 70–80-yr-old semi-natural British woodlands (Patenau et al. 2003). According to provisional benchmarks for dead wood in British forests (Kirby et al. 1998), Suserup Skov has a high level of dead wood (>40 m\(^3\) ha\(^{-1}\)). Such high levels of dead wood are characterized as uncommon and found in forests likely to be long (>70 yr) unmanaged and/or to have been affected by major disturbance. These properties of British forests with high levels of dead wood are well in line with the management history of Suserup Skov (Heilmann-Clausen et al. 2007).

The forest floor C stock (4.5 Mg ha\(^{-1}\)) was relatively small at this site which can be attributed to the nutrient-rich mineral soil. Decomposition is rapid (Ritter and Bjørnlund 2005), and forest floor accumulation of C is correspondingly low. The C stock of the forest floor was comparable to C stocks found in beech stands at similar soil types in Denmark whereas beech stands can accumulate three times as much C in forest floors at poor, sandy soil types (Vesterdal and Raulund-Rasmussen 1998).

The mineral soil stored a relatively large amount of C to 1 m depth at Suserup (132 Mg ha\(^{-1}\), Vejre et al. (2003) reported a mean value for well-drained Danish forest soils of 125 Mg C ha\(^{-1}\), but the mean value for the dominant soil type at Suserup (Alfsols) was only 88 Mg C ha\(^{-1}\). The soils at Suserup Skov are quite representative of Danish Alfsols with respect to particle size distribution and pedological development, so this is not the primary cause for the higher C content. Although the C content in some of the profiles may have been overestimated slightly because of larger stones not accounted for, the C content at Suserup is well above the average for the soil type. The high input of organic matter to soils because of limited harvesting has been stressed as a factor contributing to maintenance of soil organic C at Suserup (Vejre and Emborg 1996).

The total C stock and relative contributions of various C pools

The total C stock estimated for this part of Suserup Skov amounted to 382 Mg ha\(^{-1}\), which is a fairly high amount compared to 80-yr-old deciduous stands in Belgium (ca 325 Mg ha\(^{-1}\), Vande Walle et al. 2001). In Suserup Skov, biomass contributed the most to the C stock, followed by mineral soil, dead wood and forest floor. Although the C

| Above- and belowground biomass (d>3 cm) | 225 | 59 |
| Dead wood (d>5cm) | 21 | 6 |
| Forest floor | 4.5 | 1 |
| Mineral soil to 1 m | 132 | 34 |
| Total | 382 | 100 |

Table 4. The distribution of C among the studied ecosystem compartments.
stock of dead wood was relatively small it made up 6% of the total C stock and was more important in this forest ecosystem than forest floor C. This is in line with results from natural North American coniferous forests, where the dead wood pool accounted for between 2 and 17% of the total C stock (Kueppers et al. 2004). Comparable contributions of the dead wood component were reported for natural Nothofagus forests in both New Zealand (7%, Hart et al. 2004) and in Argentina (11%, Weber 1999).

The relative contribution of dead wood and soil pools obviously depends on soil type, forest type, age and developmental stage of the forest stand. The relative contribution of soils to the total C pool was much larger in a British semi-natural deciduous forest (ca 70%) due to much higher mineral soil C stocks (335 Mg ha\(^{-1}\) to 50 cm depth) and lower dead wood and biomass C pools in these 70–80-yr-old forests (Patenaude et al. 2003). For Pacific Northwest coniferous forests, Sun et al. (2004) reported that the relative contribution of necromass C pools (mineral soil, forest floor and dead wood C) decreased as a negative exponential function of stand age to a value of around 35% for stands aged 150–200 yr. In Suserup, these necromass pools made up 41% of total C which is fairly consistent with the findings of Sun et al. (2004).

This study has contributed with a rough estimate of the C stock and C stock distribution in a natural beech-dominated forest in Denmark. The study was not based on a specific inventory of C stocks and needed to rely on standard mensuration methods for quantification of biomass C stocks as destructive sampling is not possible in the forest reserve. The C stock in soils must be regarded with caution, as it is only based on four soil pits, but also the biomass C stock has high uncertainty due to the use of a standard biomass expansion factor for broadleaves used in Danish UNFCCC reporting (Illerup et al. 2005). There are currently no available expansion functions to estimate belowground biomass more accurately under Danish conditions. Regeneration trees with a diameter < 3 cm and ground vegetation were not included, but ground vegetation generally contributes little to the total C stock (Weber 1999, Vande Walle et al. 2001, Patenaude et al. 2003). In spite of these shortcomings, the study has indicated the large potential for C storage in such beech-dominated forest reserves on nutrient-rich till soils. The high C stock in semi-natural forests also suggest that more C could be stored by conversion from the traditional forest management system based on clearcutting and replanting to continuous cover forestry with focus on the maintenance of the dead wood component.

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