Suserup 1992-2002 Structural Dynamics, Developmental Phases and Storm Damage
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Suserup 1992-2002
Structural Dynamics, Developmental Phases and Storm Damage

Jaris Bigler, Morten Christensen, Katrine Hahn & Anders Busse Nielsen
Suserup Skov in Denmark represents the semi-natural mixed deciduous forest on the better soils in eastern Denmark where beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), oak (*Quercus robur*) and elm (*Ulmus glabra*) are common species. The site has more or less been continuously forested for the last 6,000 years (Hannon *et al.* 2000) and has stayed free of intensive silvicultural management. Suserup Skov is one of the best places for research on dynamics and processes in mixed deciduous semi-natural forests in Denmark.

In 1992, an intensive monitoring programme took place, which resulted in a complete forest inventory, detailed measurements in a 1-ha permanent plot (Emborg unpublished), mapping of the developmental phases (Emborg *et al.* 1996), soil mapping (Vejre and Emborg 1996), an outline of the management history of Suserup (Fritzbøger and Emborg 1996), and the development of a model of the cyclic dynamics (Emborg *et al.* 2000).

The 2002-remeasurement programme provided the same type of information about the status of the forest as the 1992-survey. In addition to these results it is now possible to describe some of the dynamic processes that have formed the development of the forest over the last 10 years.

In this report we present the results of the re-measurement 10 years after the first survey, including results on the effect of the severe storm that hit the region in December 1999.
2 Materials and methods

2.1 Site

Suserup Skov (55°22’ N, 11°34’ E) is a semi-natural, mixed deciduous forest, situated on the northern side of lake Tystrup in central Zealand, Denmark.

The climate is cool-temperate, sub-oceanic with an annual mean temperature of 8.1° C and an annual mean precipitation of 635 mm with a maximum occurring in July to December (Frich et al. 1997, Laursen et al. 1999). The terrain of Suserup Skov is primarily an undulating elevated plateau to the north with 10-15% slopes down towards a lower terrace along the lakeside. The low terrace consists of lacustrine soils, developed through a slow land reclamation process along the lakeside, which is caused by accumulation of organic material, intermingled with pockets of sediments rich in clay. The elevated parts are mainly developed from glacial calcareous till (Vejre and Emborg 1996). The forest comprises 19.2 ha and consists of three parts (A, B and C) with different management histories (Emborg et al. 1996). The forest became a non-intervention forest reserve in 1925 (Fritzbøger & Emborg and 1996).

Part A (10.7 ha) is dominated by beech (Fagus sylvatica), but ash (Fraxinus excelsior) and wych elm (Ulmus glabra) are also common species. A model for the dynamics occurring in this part of the forest was proposed by Christensen et al. (1993) and Emborg et al. (1996, 2000). Five phases were defined and mapped in the 1992-survey (Emborg et al. 2000): Degradation (degradation phase), Innovation (regeneration phase), Aggradation (building phase), Early Biostatic (mature phase) and Late Biostatic (ageing phase).

Part B (4.9 ha) has a history of forest grazing. The more open conditions resulted in an oak-dominated (Quercus robur) canopy layer. Sycamore maple (Acer pseudoplatanus) is most abundant in this part of the forest, due to presence of a seed source just outside the forest.

Part C (3.7 ha) is situated along the lakeside, and is dominated by alder (Alnus glutinosa) on the wettest conditions and beech on the more elevated sites.

2.2 Scientific recordings

The recordings in Suserup Skov were done with a 10-year interval in 1992 and in 2002. The recordings included a 1) complete inventory of the entire forest, 2) phase mapping in part A, and 3) recordings in permanent plots, which were all done in both years. A more specific study on the impact of the latest storm took place in 2000 (Table 2.1). In addition to the here listed recordings, numerous studies on topics such as flora, fungi, fauna, natural regeneration, soil ecology, water household and lake ecology have been carried out during the last decades.
### Table 2.1 – Overview of scientific recordings in Suserup Skov from 1992 to 2002.

<table>
<thead>
<tr>
<th>Year</th>
<th>Extension of recording</th>
<th>Description of field work</th>
<th>Chapter</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>Entire forest</td>
<td>Trees with a dbh &gt;29 cm were measured with a measuring tape showing girth and positioned and exact dbh noted. The condition of the tree were noted as either alive and fit, weak, extremely weak or dead</td>
<td>3</td>
</tr>
<tr>
<td>1992</td>
<td>Entire forest</td>
<td>All trees alive and with a dbh &gt;3 cm were measured (n=18451) with a calliper and noted in 2-cm classes {4;6;8…28 cm}</td>
<td>4</td>
</tr>
<tr>
<td>1992</td>
<td>Part A</td>
<td>Mapping of the developmental phases in part A</td>
<td>5</td>
</tr>
<tr>
<td>1992</td>
<td>Silvistar plot</td>
<td>A 0.96 ha permanent plot was established and a 3D inventory was conducted (Silvistar)</td>
<td>7</td>
</tr>
<tr>
<td>2000</td>
<td>Entire forest</td>
<td>After the gale 3rd of December 1999 all trees with a dbh &gt;15 cm that were partly or totally uprooted or broken at branch or trunk level were recorded with position, fall direction, damage type, cause of damage (direct wind or other fallen trees) and other interactions with neighbouring trees and finally the dimensions of the soil disturbance</td>
<td>6</td>
</tr>
<tr>
<td>2002</td>
<td>Entire forest</td>
<td>Trees with a dbh &gt;29 cm were measured with a measuring tape showing girth and positioned and exact dbh noted. The condition of the tree were noted as either alive and fit, weak, extremely weak or dead</td>
<td>3</td>
</tr>
<tr>
<td>2002</td>
<td>Permanent plots</td>
<td>All trees alive and with a dbh &gt;3 cm were re-measured in 2002 in 3 permanent 1 ha plots</td>
<td>4</td>
</tr>
<tr>
<td>2002</td>
<td>Part A</td>
<td>Re-mapping of the developmental phases in part A</td>
<td>5</td>
</tr>
<tr>
<td>2002</td>
<td>Silvistar plot</td>
<td>Re-mapping of the Silvistar plot</td>
<td>7</td>
</tr>
</tbody>
</table>

1All measurements were completed within 50x50 m fields based on a grid previously laid out in the forest.

### 2.3 Tree species in Suserup Skov

- **Acer plantanoides** L. – norway maple
- **Acer pseudoplatanus** L. – sycamore maple
- **Aesculus hippocastanum** L. – horse chestnut
- **Alnus glutinosa** (L.) Gaertner - alder
- **Betula pendula** Roth. – silver birch
- **Corylus avellana** L. - hazel
- **Crataegus laevigata** (Poiret) DC. - hawthorn
- **Crataegus monogyna** Jacq. - hawthorn
- **Euonymus europaeus** L. - spindle
- **Fagus sylvatica** L. - beech
- **Fraxinus excelsior** L. - ash
- **Malus sylvestris** Miller – crap apple
- **Quercus robur** L. – pedunculate oak
- **Prunus avium** L. – wild cherry
- **Sorbus aucuparia** L. - rowan
- **Sambucus nigra** L. - elder
- **Salix caprea** L. – goat willow
- **Salix cinerea** L. – grey willow
- **Tilia platyphyllos** Scop. – broad-leaved lime
- **Ulmus glabra** Hudson – wych elm
3 Entire forest inventory

Jaris Bigler

3.1 Introduction

In this chapter, the results from the inventory of the entire forest in 2002 are described and compared to the results from the 1992-recording. The results primarily concern three topics 1) living and dead trees, 2) changes in species composition, and 3) growth, represented in the three parts, A, B, and C of the forest.

3.2 Method and materials

3.2.1 The site

Suserup Skov is divided into three parts, denoted A, B and C, as described in chapter 2.1. The subdivision is based on differences in former management schemes, edaphical conditions, and species composition. For more details see Emborg et al. (1996).

3.2.2 Measurements

In both 1992 and 2002, all trees with a dbh greater than 29 cm in the forest were positioned using a 50x50 m grid. If an individual consisted of more than one stem, and a calculated summarised basal area (BA) for this stem exceeded 29 cm dbh, the individual was included. If the stem was not vertical, the diameter was measured at 1.3 m height from the basis of the tree. For each 2500 m² (50x50 m grid) a list of all vascular plants was made. The time used for the 2002-recording was approximately 15 days of two persons working 7 hours a day (210 hours). In between those two major surveys, damaged and dead trees were recorded on an annual basis.

3.2.3 Calculations

The d/h-regressions were constructed after the 1992-survey based on the equation:

\[ h = H_{\text{dom}} \cdot \left( \frac{d}{d + k} \right)^3 + 1.3 \]  

(regression 3.1)

where \( h \) = tree height; \( d \) = dbh; \( H_{\text{dom}} \) = dominant (maximum) tree height and \( k \) = constant determining the inflection point of the sigmoid curve.

For ash the regression was determined to:

\[ h = 41 \cdot \left( \frac{d}{d + 5.16} \right)^3 + 1.3, \]  

(regression 3.2)

and for beech to:

\[ h = 41 \cdot \left( \frac{d}{d + 6.46} \right)^3 + 1.3. \]  

(regression 3.3)

The d/h-regression for oak was graphically estimated (n=31). All other species were pooled to compute a common d/h-regression (n=215):

\[ h = 30 \cdot \left( \frac{d}{d + 4.89} \right)^3 + 1.3. \]  

(regression 3.4)

The form factors used in the 1992 survey were for all trees < 31 cm dbh (except oak) as shown in table 3.1 for trees up to 49 cm dbh it was 0.60 and for trees larger than 49 cm dbh it was 0.59.

<table>
<thead>
<tr>
<th>DBH</th>
<th>Form factor</th>
</tr>
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<tbody>
<tr>
<td>4</td>
<td>0.78</td>
</tr>
<tr>
<td>6</td>
<td>0.72</td>
</tr>
<tr>
<td>8</td>
<td>0.68</td>
</tr>
<tr>
<td>10</td>
<td>0.66</td>
</tr>
<tr>
<td>12</td>
<td>0.65</td>
</tr>
<tr>
<td>14</td>
<td>0.64</td>
</tr>
<tr>
<td>16</td>
<td>0.63</td>
</tr>
<tr>
<td>18</td>
<td>0.62</td>
</tr>
<tr>
<td>20</td>
<td>0.62</td>
</tr>
<tr>
<td>22</td>
<td>0.62</td>
</tr>
<tr>
<td>24</td>
<td>0.61</td>
</tr>
<tr>
<td>26</td>
<td>0.61</td>
</tr>
<tr>
<td>28</td>
<td>0.61</td>
</tr>
<tr>
<td>30</td>
<td>0.60</td>
</tr>
</tbody>
</table>

Table 3.1 – Form factor for trees < 31 cm DBH.

For oak ≤ 105 cm dbh the volume were derived directly from the volume table (Madsen 1987), and for all oaks > 105 cm dbh the form factor was estimated to be 0.63.

Single tree volume was calculated as

\[ V = h \cdot BA \cdot f, \]  

(regression 3.5)

Where \( V \) = volume of the tree; \( h \) = height of the tree; \( BA \) = Basal Area of the tree and \( f \) = form factor between the calculated cylinder and the model tree.

These regressions and form factors were used for the volume calculations in both 1992 and 2002, to secure comparability.
3.3 Results

3.3.1 Status of the forest
The living volume of part A in Suserup Skov (566 m³) is close to a north European average, whereas part B (734 m³) and part C (648 m³) contain rather large volumes of living trees (Table 3.2).

The forest as a whole has an atypical volume distribution (figure 3.1), reflecting heterogeneity in the structure of the different parts as well as the former management. The overall impression is that the shape of the curve is maintained from 1992 to 2002, but has shifted rightwards due to growth. The cohorts of trees are still clearly visible.

Figure 3.2 provides a closer look at the distribution of dying trees in time. The large majority of those damages, which have lead to death in the 10-year period, are linked to the storm of December 3rd 1999. More trees are expected to die from storm-related damages within the next years.

3.3.2 Changes in living and dead wood volume 1992-2002
The average increase of 3% in the standing living volume from 1992 to 2002, is a combination of a small decrease in part A and B, but a great increase in part C (Table 3.3). The changes in part A and B are relatively small, indicating that these parts of the forest are closer to a dynamic equilibrium than part C, which in the same period experienced a dramatically increase in volume. In part A and B, the loss of especially beech was not counterbalanced by the increase in standing volume and the volume of new trees. In part C, the volume gained by the growth of existing trees and the large increase in the volume of new trees largely exceeded the volume of the trees dying in the same period. The changes in growth are analysed with respect to species within each part of the forest in the next sections.

Figure 3.2 - Volume of trees dead 1992-2002. NOTE: Year denotes year of damage leading to the death of the tree – not year of death. For 578 m³ corresponding to 29 % of the total dead wood volume, it was not possible to date the year of damage.

3.3.3 Overall changes in species 1992-2002
The basal area of living trees is almost constant from 1992 to 2002 in part A and B of the forest, whereas the basal area in part C is still increasing (Table 3.3). For oak, the basal area is declining, whereas the basal area of ash is increasing in all three parts of the forest. Sycamore maple is expanding rapidly in part B and alder shows a similar behaviour in part C, with both species almost doubling their basal area. Moreover, sycamore maple nearly doubles the number of individuals at the same time. The increase in basal area of alder in part C is mainly due to existing stems growing larger. Although dutch elm disease was first observed in the forest in 1995, it was only possible to detect a decrease in the volume of wych elm in part B.

3.3.4 Changes in part A 1992-2002
Part A experienced a moderate decrease in terms of volume from 1992 to 2002 but in the same period the basal area remained stable and stem density increased. Ash, lime, and wych elm all increased in both stem density and volume, whereas beech decreased in terms of volume but increased in terms of stem density, meaning that mostly larger individuals died in the recording period. Oak decreased in both volume and stem density (Table 3.4).

The volume-based over-representing of large diameter classes, which was clearly visible in 1992 (figure 3.3) is to some extent levelled out.
Table 3.2 - Table 3.2 Suserup and other forests of northwestern Europe. Data marked with * are estimated volumes of all trees exceeding a minimum dbh of 3 cm. The data is multiplied by a factor that is based on data from the 1992 survey in Suserup.


<table>
<thead>
<tr>
<th>Site</th>
<th>sub site</th>
<th>Country</th>
<th>Total volume pr. Ha</th>
<th>Minimum DBH [cm]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bieszczady Mts</td>
<td>Rabia Skala I</td>
<td>Poland</td>
<td>257</td>
<td></td>
</tr>
<tr>
<td>Bieszczady Mts</td>
<td>Moczarne I</td>
<td>Poland</td>
<td>391</td>
<td></td>
</tr>
<tr>
<td>Serrahn</td>
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<td>Germany</td>
<td>458</td>
<td>7(6)</td>
</tr>
<tr>
<td>Kyjov</td>
<td></td>
<td>Slovakia</td>
<td>464</td>
<td>6</td>
</tr>
<tr>
<td>Strodam Reserve</td>
<td>Strøgaardsvang</td>
<td>Denmark</td>
<td>465</td>
<td></td>
</tr>
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<td></td>
<td>Slovakia</td>
<td>465</td>
<td>6</td>
</tr>
<tr>
<td>Fauler Ort</td>
<td></td>
<td>Germany</td>
<td>481</td>
<td>7(6)</td>
</tr>
<tr>
<td>Kyjov</td>
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<td>490</td>
<td></td>
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<tr>
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<td>6</td>
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<tr>
<td>Heiligen Hallen</td>
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<td>Germany</td>
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<td>7(6)</td>
</tr>
<tr>
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<td>Bieszczady Mts</td>
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<td>Vilm</td>
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<td><strong>Suserup</strong></td>
<td><strong>Part A</strong></td>
<td><strong>Denmark</strong></td>
<td>566 (674)*</td>
<td>29 (3)</td>
</tr>
<tr>
<td>Stuzica 4</td>
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<td>Slovakia</td>
<td>569</td>
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<td><strong>Suserup</strong></td>
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<td>29 (3)</td>
</tr>
<tr>
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<td></td>
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<td></td>
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<tr>
<td><strong>Suserup</strong></td>
<td><strong>Part B</strong></td>
<td><strong>Denmark</strong></td>
<td>734 (874)*</td>
<td>29 (3)</td>
</tr>
<tr>
<td>Havesova</td>
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<td>Slovakia</td>
<td>736</td>
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</tr>
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<td>Rozok</td>
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<td>6</td>
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<tr>
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<td>Rozok</td>
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<tr>
<td><strong>Average</strong></td>
<td></td>
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<td>597</td>
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<table>
<thead>
<tr>
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<tbody>
<tr>
<td>A (10.7 ha)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fráxinus excélsior</td>
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<td>81.1</td>
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<td>12.8</td>
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<td>5.1</td>
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<tr>
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<td>7.3</td>
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<td>0.0</td>
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<td>5.7</td>
<td>7.3</td>
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<tr>
<td>Other species</td>
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<td>3.8</td>
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<td>0.0</td>
<td>1.9</td>
</tr>
<tr>
<td>Total</td>
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<td>566.0</td>
<td>49.6</td>
<td>122.5</td>
<td>53.8</td>
</tr>
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<td>B (4.9 ha)</td>
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<td>Acer pseudoplatanus</td>
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<td>-4.5</td>
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<tr>
<td>Other species</td>
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<td>4.6</td>
<td>1.6</td>
<td>0.6</td>
<td>-2.1</td>
</tr>
<tr>
<td>Total</td>
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<td>734.1</td>
<td>47.2</td>
<td>94.0</td>
<td>37.8</td>
</tr>
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<td>C (3.7 ha)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alnus glutinosa</td>
<td>89.8</td>
<td>209.7</td>
<td>16.1</td>
<td>2.5</td>
<td>106.3</td>
</tr>
<tr>
<td>Fráxinus excélsior</td>
<td>99.6</td>
<td>129.1</td>
<td>9.3</td>
<td>4.8</td>
<td>25.0</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>247.9</td>
<td>251.8</td>
<td>22.2</td>
<td>28.2</td>
<td>9.9</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>38.1</td>
<td>28.0</td>
<td>0.0</td>
<td>10.9</td>
<td>0.8</td>
</tr>
<tr>
<td>Ulmus glabra</td>
<td>5.4</td>
<td>12.6</td>
<td>12.2</td>
<td>7.3</td>
<td>2.4</td>
</tr>
<tr>
<td>Other species</td>
<td>4.1</td>
<td>16.5</td>
<td>7.5</td>
<td>0.3</td>
<td>5.3</td>
</tr>
<tr>
<td>Total</td>
<td>484.9</td>
<td>647.7</td>
<td>67.3</td>
<td>53.9</td>
<td>149.5</td>
</tr>
<tr>
<td>Whole forest (19.3 ha)</td>
<td>606.0</td>
<td>624.3</td>
<td>52.4</td>
<td>102.1</td>
<td>68.1</td>
</tr>
</tbody>
</table>

by 2002, mainly due to the 1999-storm. Although there is a lack of information about trees smaller than 29 cm dbh, the figure indicates a gradual rise in the volume of smaller trees, compensating for the low volume in the 40-70 cm diameter classes.

3.3.5 Changes in part B 1992-2002
Part B experienced a decrease in volume from 1992 to 2002. In the same period basal area remained stable and the stem density increased. Sycamore maple almost doubled in volume, basal area and stem density and also ash expanded, but less rapidly. The volume of beech decreased but the stem density increased, meaning that large individuals have died and are being replaced by a steady recruitment. Oak decreased in volume as well as stem density. The density of large wych elm trees declined but is compensated by a high recruitment rate (Table 3.5).

3.3.6 Changes in part C 1992-2002
The total volume and basal area increased rapidly in part C from 1992 to 2002, but the stem density did not increase at the same rate. The existing stems of alder increased in both volume and basal area, and a few new stems have grown larger than 29 cm dbh from 1992 to 2002. Ash, beech and wych elm (and »other species« of which sycamore maple and broad-leaved lime are the most important) all increased in volume, basal area and stem density. Oak decreased due to death of a few large individuals (Table 3.6).
Table 3.4 – Table 3.4 Volume of living trees (m³/ha), BA of living trees (m²/ha), and stem density of trees >29 cm dbh (n/ha) in 1992 and 2002 in part A. Other species include: Aesculus hippocastanum, Alnus glutinosa, Acer pseudoplatanus, Corylus avellana, and Prunus avium.

<table>
<thead>
<tr>
<th>Year</th>
<th>Volume/ha</th>
<th>BA/ha</th>
<th>n/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>Fraxinus excelsior</td>
<td>66.5</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>Fagus sylvatica</td>
<td>394.2</td>
<td>18.9</td>
</tr>
<tr>
<td></td>
<td>Quercus robur</td>
<td>113.9</td>
<td>5.6</td>
</tr>
<tr>
<td></td>
<td>Tilia platyphyllos</td>
<td>5.7</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Ulmus glabra</td>
<td>3.1</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Other species</td>
<td>1.6</td>
<td>0.1</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>585.1</td>
<td>28.7</td>
</tr>
<tr>
<td>2002</td>
<td>Fraxinus excelsior</td>
<td>81.1</td>
<td>4.3</td>
</tr>
<tr>
<td></td>
<td>Fagus sylvatica</td>
<td>369.7</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td>Quercus robur</td>
<td>98.4</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>Tilia platyphyllos</td>
<td>7.3</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>Ulmus glabra</td>
<td>5.7</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Other species</td>
<td>3.8</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>566.0</td>
<td>29.0</td>
</tr>
</tbody>
</table>

Table 3.5 – Table 3.5 Volume of living trees (m³/ha), BA (m²/ha) and stem density of trees > 29 cm dbh (n/ha) in 1992 and 2002 in part B. Other species include: Aesculus hippocastanum, Alnus glutinosa, Acer pseudoplatanus, Corylus avellana, and Prunus avium.

<table>
<thead>
<tr>
<th>Year</th>
<th>Volume/ha</th>
<th>BA/ha</th>
<th>n/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>Acer pseudoplatanus</td>
<td>10.6</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>Fraxinus excelsior</td>
<td>149.6</td>
<td>7.5</td>
</tr>
<tr>
<td></td>
<td>Fagus sylvatica</td>
<td>238.3</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>Quercus robur</td>
<td>316.4</td>
<td>16.2</td>
</tr>
<tr>
<td></td>
<td>Ulmus glabra</td>
<td>22.6</td>
<td>1.6</td>
</tr>
<tr>
<td></td>
<td>Other species</td>
<td>5.8</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>743.2</td>
<td>38.2</td>
</tr>
<tr>
<td>2002</td>
<td>Acer pseudoplatanus</td>
<td>20.7</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>Fraxinus excelsior</td>
<td>160.2</td>
<td>8.0</td>
</tr>
<tr>
<td></td>
<td>Fagus sylvatica</td>
<td>224.8</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>Quercus robur</td>
<td>304.8</td>
<td>15.3</td>
</tr>
<tr>
<td></td>
<td>Ulmus glabra</td>
<td>19.0</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Other species</td>
<td>4.6</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>734.1</td>
<td>38.3</td>
</tr>
</tbody>
</table>

Table 3.6 – Table 3.6 Volume of living trees (m³/ha¹), Basal Area per ha (m²/ha¹) and number of trees > 29 cm dbh pr. ha in 1992 and 2002 in part C. Other species included: Acer pseudoplatanus, Betula pendula, Corylus avellana, Crataegus sp., Salix sp., and Tilia platyphyllla.

<table>
<thead>
<tr>
<th>Year</th>
<th>Volume/ha</th>
<th>BA/ha</th>
<th>n/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>Alnus glutinosa</td>
<td>89.8</td>
<td>6.6</td>
</tr>
<tr>
<td></td>
<td>Fraxinus excélsior</td>
<td>99.6</td>
<td>5.0</td>
</tr>
<tr>
<td></td>
<td>Fagus sylvatica</td>
<td>247.9</td>
<td>12.1</td>
</tr>
<tr>
<td></td>
<td>Quercus robur</td>
<td>38.1</td>
<td>2.0</td>
</tr>
<tr>
<td></td>
<td>Ulmus glabra</td>
<td>5.4</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>Other species</td>
<td>4.1</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>484.9</td>
<td>26.5</td>
</tr>
<tr>
<td>2002</td>
<td>Alnus glutinosa</td>
<td>209.7</td>
<td>14.1</td>
</tr>
<tr>
<td></td>
<td>Fraxinus excélsior</td>
<td>129.1</td>
<td>6.4</td>
</tr>
<tr>
<td></td>
<td>Fagus sylvatica</td>
<td>251.8</td>
<td>13.0</td>
</tr>
<tr>
<td></td>
<td>Quercus robur</td>
<td>28.0</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>Ulmus glabra</td>
<td>12.6</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Other species</td>
<td>16.5</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>647.7</td>
<td>37.2</td>
</tr>
</tbody>
</table>

3.3.6 Changes in growth 1992-2002
When examining the trees alive in the 2002-survey for their growth in the 10-year period, there seems to be a quite high difference between species in terms of both diameter, basal area and volume increment. One example of diameter increment for ash is given in figure 3.4. Oak and alder represent the two extremes of relative volume increment in Suserup Skov, with alder having an almost 20-fold higher relative volume increment than oak (Table 3.7). The volume increment patterns are shown in figure 3.5. The high growth of alder, which typically consists of many stems, is a result of the release of former coppice management. The slow growth of oak is explained by the overrepresentation of very large and old single-stemmed trees with reduced vitality.
3.4 Discussion

3.4.1 Part A
The 1999-storm resulted in a decrease in living volume. The storm mainly blew down those large trees, which made up the over-representation in terms of volume in 1992. This phenomenon explains why the total stem density in the same period increased: The density of new small trees increased and the storm killed a low number of very large trees – predominantly beech and oak. Both of these species were over-represented in the larger diameter classes due to former forest management schemes (Emborg et al. 1996). Smaller trees of beech, ash, broad-leaved lime and wych elm increased in stem density and the last three also in volume. These smaller trees were not as exposed to storm damage as the larger ones and their numbers are increasing. The general trend of rejuvenation of part A is also reflected in the pattern of developmental phase as demonstrated in chapter 5. This rejuvenation is resulting in an increase of especially ash. Broad-leaved lime is expanding and is believed to continue to do so especially on the low-lying sites until a natural equilibrium is reached. A one ha permanent plot placed in this area is described in detail in chapter 4.

3.4.2 Part B
The general decline of oaks is also present in part B and dutch elm disease has also caused a beginning decline of larger elm trees. The beginning rejuvenation of part B results in a high recruitment rate of mainly sycamore maple but also ash, beech, and wych elm. Sycamore maple will probably continue to expand until a natural equilibrium is reached. The overall result of the recruitment of shade-tolerant species like sycamore maple and beech may be a more dense and dark forest, which will lead to a change in the competitive situation between the species in the future. To get a closer look at the competition strength of sycamore maple, we included the trees smaller than 29 cm in the survey of a permanent plot, see chapter 4.

3.4.3 Part C
Part C is a mixture of former meadows (grazed until about 1925) former alder-coppice (last coppice about 1880) and older beech-dominated stands on the elevated parts. Due to the rather intensive former management, part C is still in a state of volume built-up. A large cohort of alder, which was established on the former meadows shortly after grazing stopped, increases in volume, and the coppice-alders are still recovering from the last cutting. It is expected that the cohort will reach a maximum in volume within the next decade or two, as some of the older alders show signs of decay resulting in dying and dead trunks. Oak shows the same signs of decline as in the other forest parts. All other species increase in numbers basal area and volume. Emborg et al. (1996) suggested a primary succession from alder to ash, but this succession is not yet visible among trees larger than 29 cm dbh.

3.4.4 General trends
Apart from the cyclic dynamics in the forest and the derived variations from equilibrium, there are some trends of general importance for the entire
forest. Oak continues to decline, but the rate is slow and it is expected to remain an important component of the forest structure for centuries due to the longevity of the species. Dutch elm disease causes increased mortality of larger wych elm trees, but the regeneration of the wych elm is on the other hand still vigorous and it is believed to continue until the disease has killed the large majority of the seed sources. The cohort of old beech trees originating from regeneration taking place after the enclosure of the forest in 1807 (Emborg et al. 1996) is more susceptible to storm damage than other size classes, and the bell-shaped group around 80-90 cm diameter as described by Emborg et al. (1996) seems to level out slowly. In accordance with the increased mortality of large, dominating beech trees a general rejuvenation takes place. This makes ash play an increasingly important role in the forest. The impact of the storm is significant but of minor importance. Especially the lakeside region is more or less unaffected, with a continually increasing standing volume.
4 Permanent plots

Jaris Bigler

4.1 Introduction

In order to obtain more precise information about regeneration and mortality among smaller trees (< 30 cm dbh) than the entire forest inventory provided (chapter 3), all trees larger than 3 cm dbh were counted for each 50x50 m grid-square in the forest in 1992. It was, however, decided that the resource consumption was too high to repeat this for the entire forest in 2002. Therefore, three permanent plots of each 1 ha were selected for detailed research. The plots were chosen, with the aim of:

- Monitoring the two potentially invasive species Acer pseudoplatanus (sycamore maple) and Tilia platyphyllos (broad-leaved lime)
- Representing the two major types of management history, 1) forest-grazing and 2) low-intensity management
- Representing the low-lying soils as well as the elevated parts of the forest

Furthermore, all plots should be as isolated as possible from the effects of the surrounding open areas (lake and farmland).

4.2 Materials and methods

4.2.1 Sites

Plot A1 (figure 4.1) is situated on the elevated slopes of part A (see chapter 2 for a description of the forest). The soil consists of loamy till (Vejre and Emborg 1996). Beech, ash, and elm dominate the site. Six rather large oak trees are also present (table 4.1).

Plot A2 (figure 4.1) is situated on the flat lower soils consisting of lacustrine clay and lacustrine sand (Vejre and Emborg 1996). The tree species composition is very similar to the one in A1, but with fewer ash trees and a significant proportion of broad-leaved lime. The origin of those broad-leaved lime trees in the forest is uncertain. Hannon et al. (2000) showed that both Tilia platyphyllos and Tilia cordata were present in the forest around 5000 years before present, but both disappeared from the pollen record before 1100 years ago. Emborg et al. (1996) suggest that the present broad-leaved lime trees are introduced/planted. Plot A1 and A2 are both situated in that part of the forest (A), which has experienced least intensive forest management.

Plot B (figure 4.1) has a somewhat different management history and was grazed until the enclosure in 1807 (Emborg et al. 1996). This is reflected in the species composition with a rather large amount of large oak trees with short boles.
and hawthorn and crap apple present in the understorey. Sycamore maple has established in this part of the forest from seeds originating from large trees situated north-east of the forest (Christensen et al. 1993).

### 4.2.2 Measurements

In 1992, all trees alive and with a dbh exceeding 3 cm (n=18451) were noted in 2-cm classes {4;6;8…28 cm}. Trees larger than 29 cm dbh were positioned and exact dbh noted. For all trees dbh was measured with a measuring tape showing girth as well as dbh. All measurements were carried out within each 50x50 m grid. This method was replicated in 2002 in the three 1-ha permanent plots, as described above (figure 4.1). In 2002, diameters of all trees alive (including lying and leaning trees) were measured using a diameter-measuring tape, and each tree noted in a scheme. Standing dead trees were noted with a special signature. Two persons were able to complete the measurements in approximately 7 hours each per ha.

### 4.3 Results

#### 4.3.1 Permanent plot A1

From 1992 to 2002, the basal area changed just slightly for trees smaller than 31 cm dbh (table 4.2). In the same period, stem density decreased with 16 %. The increase in the total basal area of beech is caused by an increase in the number of large trees (dbh >18 cm), whereas the number of small beech trees has decreased (figure 4.3). In contrast, both ash and elm smaller than 30 cm dbh have decreased in basal area as well as stem density (figure 4.4 and 4.5).

Trees larger than 31 cm dbh appear to grow quite well. Three beech trees which blew down in the 1999-storm caused an insignificant decrease in basal area. Two of these trees are the reason for the appearance of Innovation phase areas, which showed up at the 2002 phase mapping (figure 4.2).

The distribution of phases indicates that the Aggradation and Early Biostatic phases were over-represented compared to the average of the forest already back in 1992, and that the major change since then is a shift in phases from Aggradation towards Early Biostatic. The changes in diameter distributions for beech,

### Table 4.1 - Basal area and number of individuals alive and larger than 3 cm dbh in the 1992-survey in the three permanent plots. “Other species” denotes:

<table>
<thead>
<tr>
<th>Species</th>
<th>A1 (m² ha⁻¹)</th>
<th>A2 (m² ha⁻¹)</th>
<th>B (m² ha⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer pseudoplatanus</td>
<td>0.0 (0)</td>
<td>0.0 (0)</td>
<td>6.5 (145)</td>
</tr>
<tr>
<td>Fagus sylvatica</td>
<td>17.6 (416)</td>
<td>18.6 (240)</td>
<td>16.4 (128)</td>
</tr>
<tr>
<td>Fraxinus excelsior</td>
<td>8.7 (162)</td>
<td>1.2 (27)</td>
<td>5.0 (43)</td>
</tr>
<tr>
<td>Quercus robur</td>
<td>8.0 (6)</td>
<td>5.4 (4)</td>
<td>15.5 (13)</td>
</tr>
<tr>
<td>Tilia platiphylos</td>
<td>0.0 (0)</td>
<td>5.5 (68)</td>
<td>0.0 (2)</td>
</tr>
<tr>
<td>Ulmus glabra</td>
<td>2.5 (317)</td>
<td>1.9 (312)</td>
<td>3.1 (472)</td>
</tr>
<tr>
<td>Other species</td>
<td>0.3 (21)</td>
<td>0.4 (28)</td>
<td>0.8 (33)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>37.0 (922)</strong></td>
<td><strong>33.0 (679)</strong></td>
<td><strong>47.3 (836)</strong></td>
</tr>
</tbody>
</table>

ash and elm are shown in figures 4.3, 4.4, and 4.5. It is of interest, that the decline of the recruitment rate of ash was visible already back in 1992.

### 4.3.2 Permanent plot A2

In plot A2, the total basal area and the stem density of trees smaller than 31 cm dbh remained fairly constant through time (table 4.3). The decrease of ash and beech (basal area and stem density) is counterbalanced by an increase of elm and broad-leaved lime.

For trees larger than 30 cm dbh, especially beech and oak showed a decline in basal area due to the fall of a few large individuals in the 1999-gale. Two oaks were killed by the 1999-gale and another died standing but was thrown over by the gale. A total of 13 beech trees died but 14 new were recorded. Of the dead beech trees, eight were killed by the 1999-gale, three were broken before the gale and two died standing. The loss of these large trees is reflected in the distribution of phases (figure 4.6). The total area of Early Biostatic and Late Biostatic phase declined from 1992 to 2002, and in the same period the total area of Innovation and Aggradation phase increased. This change did not lead to a significant loss of basal area and stem density of trees larger than 31 cm dbh, except for beech and oak.

<table>
<thead>
<tr>
<th>BA and (n)</th>
<th>Fagus</th>
<th>Fraxinus</th>
<th>Quercus</th>
<th>Ulmus</th>
<th>Other species</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 31 cm DBH</td>
<td>5.50</td>
<td>3.99</td>
<td>0.00</td>
<td>2.63</td>
<td>0.39</td>
<td>12.51</td>
</tr>
<tr>
<td>≥ 31 cm DBH</td>
<td>12.10</td>
<td>3.68</td>
<td>7.65</td>
<td>0.08</td>
<td>0.00</td>
<td>23.51</td>
</tr>
<tr>
<td>Total</td>
<td>17.60</td>
<td>7.67</td>
<td>7.65</td>
<td>2.71</td>
<td>0.39</td>
<td>36.20</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>BA and (n)</th>
<th>Fagus</th>
<th>Fraxinus</th>
<th>Quercus</th>
<th>Ulmus</th>
<th>Other species</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 31 cm DBH</td>
<td>6.58</td>
<td>3.75</td>
<td>0.00</td>
<td>2.33</td>
<td>0.23</td>
<td>12.89</td>
</tr>
<tr>
<td>≥ 31 cm DBH</td>
<td>11.99</td>
<td>4.20</td>
<td>7.98</td>
<td>0.13</td>
<td>0.08</td>
<td>24.38</td>
</tr>
<tr>
<td>Total</td>
<td>18.57</td>
<td>7.95</td>
<td>7.98</td>
<td>2.46</td>
<td>0.31</td>
<td>37.27</td>
</tr>
</tbody>
</table>

Table 4.2 - Basal area and number of trees < 31 cm dbh in plot A1. Other species denotes: Crataegus sp., Prunus avium, Sambucus nigra and Sorbus aucuparia.
not lead to a significant increase in the amount of small trees.

The changes in diameter distributions for beech, ash, broad-leaved lime, and elm are shown in figures 4.7, 4.8, 4.9, and 4.10. Figure 4.10 indicates a rather high recruitment rate of elm, which was not detected for the other main tree species. Already in 1992 a rapid increase in recruitment rate of elm was visible and this seems to continue in 2002. An opposite pattern is the case of beech where a general decline in recruitment rate of elm was visible and this seems to continue in 2002. Broad-leaved lime shows a more or less flat curve, indicating a stable recruitment rate, and a low mortality rate. Ash had an almost lack of recruitment except for the lowest diameter classes.

4.3.3 Permanent plot B
In the permanent plot B, the total basal area and

<table>
<thead>
<tr>
<th>BA and (n)</th>
<th>Fagus</th>
<th>Fraxinus</th>
<th>Quercus</th>
<th>Tilia</th>
<th>Ulmus</th>
<th>Other species</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt; 31 cm DBH</td>
<td>3.51</td>
<td>0.82</td>
<td>0.00</td>
<td>0.64</td>
<td>1.43</td>
<td>0.11</td>
<td>6.50</td>
</tr>
<tr>
<td>≥ 31 cm DBH</td>
<td>20.01</td>
<td>0.74</td>
<td>10.08</td>
<td>3.93</td>
<td>0.00</td>
<td>0.34</td>
<td>35.10</td>
</tr>
<tr>
<td>Total</td>
<td>23.52</td>
<td>1.56</td>
<td>10.08</td>
<td>4.57</td>
<td>1.43</td>
<td>0.45</td>
<td>41.60</td>
</tr>
<tr>
<td>2002</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt; 31 cm DBH</td>
<td>3.27</td>
<td>0.52</td>
<td>0.83</td>
<td>0.83</td>
<td>1.75</td>
<td>0.08</td>
<td>6.45</td>
</tr>
<tr>
<td>≥ 31 cm DBH</td>
<td>15.30</td>
<td>0.67</td>
<td>5.37</td>
<td>4.85</td>
<td>0.28</td>
<td>0.26</td>
<td>26.83</td>
</tr>
<tr>
<td>Total</td>
<td>18.57</td>
<td>7.95</td>
<td>7.98</td>
<td>5.68</td>
<td>2.46</td>
<td>0.31</td>
<td>42.95</td>
</tr>
</tbody>
</table>

Table 4.3 - Basal area and number of trees < 31 cm dbh in plot A2. Other species denotes Acer platanoides, Acer pseudoplatanus, Corylus avellana, Crataegus spp., Sambucus nigra, and Sorbus aucuparia.
stem density for all trees smaller than 31 cm dbh decreased by 20% and 22% respectively (table 4.4). For beech (27%), elm (26%) and ash (18%), the decrease was much faster than for sycamore maple (1%). In terms of stem density, the situation is more equal (beech 34%, elm 16%, ash 36% and sycamore maple 19%). The die back of large elm trees is mainly due to dutch elm disease.

The basal area of trees larger than 30 cm dbh increased slightly more than the corresponding decrease in basal area of trees smaller than 31 cm dbh (table 4.4). This increase is mainly due to rapidly growing ash trees and a steep increase in the number of sycamore maple. The changes in diameter distributions for sycamore maple, beech, ash, and elm are shown in figures 4.11, 4.12, 4.13, and 4.14.

### 4.4 Discussion

#### 4.4.1 General topics

The information provided by the diameter distribution of the smaller trees, resulted in detailed and species-specific knowledge about the status of the species with respect to regeneration and competitive success. Due to the presence of two surveys a dynamic dimension can be incorporated to show if trends predicted from the diameter-distributions are reflected in the development within the last 10 years. The static and the dynamic data can be interpreted together to provide us important knowledge about the role of the species in the cycle of developmental phases.

#### 4.4.2 Permanent plot A1

The distribution of phases and the diameter distribution of trees both smaller and larger than 31 cm dbh indicate that plot A1 is in a maturing stage. In this plot, the forest is growing denser, and the resulting darker light regime causes a lack of recruitment of first ash (already visible in 1992) and now also visible for elm and beech. The general increase in basal area of beech trees (17-31 cm dbh) indicates a cohort of trees that continuously grows larger but at the same time adds to the suppression of younger trees.

#### 4.4.3 Permanent plot A2

This plot is characterised by a general rejuvenation caused by the 1999-storm. In 1992 the Early Biostatic phase was over-represented in plot A2 (compared to the average of the forest) leading to a low recruitment rate of ash - a tendency now also visible for beech. The conditions has changed now, but the response is only visible in the lowest diameter classes of ash and elm, and has not yet lead to a significant increase in the amount of small trees. Broad-leaved lime seems to have a stabile and probably increasingly important role in the system. The mortality of broad-leaved lime seems to be quite low, at least on this soil type (which is not common throughout the entire forest). The high recruitment rate of elm is expected to decline when dutch elm disease kills the majority of the seed-bearing trees.

#### 4.4.4 Permanent plot B

The recordings in plot B shows that the former light-open and grazed forest is now growing denser. The basal area of the larger trees has increased slightly more than the corresponding decrease of smaller trees. Apart from some large ash trees, especially sycamore maple is responsible for the decline in light intensity, which is reflected in the low recruitment rate of all major species. Sycamore maple is an invasive species that expands rapidly on this site. Judging from the diameter distributions, the competition with ash seems to be in favour of sycamore maple. The high mortality of the larger elm trees is due...
to Dutch elm disease. Sycamore maple is taking advantage of this situation, and is believed to continue to do so. The dynamic equilibrium and potential role of sycamore maple is not reached yet.
5. Changing phases

Morten Christensen

5.1 Introduction

From the general models of the forest cycle, a specific model of the forest cycle for Suserup Skov was defined based on the survey in 1992 (Emborg et al. 2000)(figure 5.2). The specific model includes five developmental phases termed the innovation, the aggradation, the early biostatic, the late biostatic and the degradation phase, in accordance with Oldemann (1990). The objective was to develop a model, in which the phases can be defined unequivocally and distinguished from each other in the field by easily measurable criteria. The criteria for distinguishing the five phases from each other (figure 5.1) was defined before the field mapping took place, based on ecological considerations and arguments.

The survey in 2002 allows us to test the validity of the model and within the limit of only ten years of development to quantify the frequency of different development series.

5.2 Methods and materials

5.2.1 Definition of development phases

Innovation phase
The beginning of the innovation phase is defined as the moment when regeneration is well established in a gap, that is more than ca. five vital plants taller than 20 cm per m² (less for larger plants). Often ash establish first due to its pioneer features, with many wind-dispersed seeds almost every year. Beech establishes within a few years, typically after the first mast year. In addition to the tree vegetation, herbs, grasses, bushes and smaller trees find their place in the open and light conditions.

Aggradation phase
The beginning of the aggradation phase is defined as the moment when the established regeneration has the competing herbal vegetation under control, that is when the regeneration has reached a height of 3 m. The first part of the phase is often dominated by fast growing ash, but often with scattered small trees like wych elm, wild cherry and elder. Beech often dominates the lower stratum throughout the phase.

Early biostatic phase
The early biostatic phase begins when the trees have reached the upper canopy layer, that is have reached a height of 25 m. Most often ash dominates from the beginning, but during the early biostatic phase beech completely takes over the canopy stratum.

Late biostatic phase
The late biostatic phase begins when the trees becomes old, have wounds and scars, and tend to become more vulnerable to biotic and abiotic damages, that is when the trees have reached a dbh of 80 cm. Usually beech completely dominates the upper canopy stratum throughout this phase, while scattered undergrowth of wych elm and beech may occur. Towards the end of the phase the old beeches begin to degenerate, dropping even large branches creating small often short-lasting gaps in the canopy.

Degradation phase
The degradation phase begins when degrading trees causes more permanent gaps in the canopy, large enough to initiate regeneration, that is gaps >100 m², which cannot be filled by lateral ingrowth of the surrounding trees. The phase can be regarded as an interface between the late biostatic and the innovation phase. It may start suddenly as a result of wind-throw, or it may develop gradually as old trees lose vitality and eventually die. Well-established regeneration in a gap defines the end of the degradation phase and the start of a new turn of the forest cycle (figure 5.2).
5.2.2 Mapping of the shifting mosaic

The shifting mosaic was field-mapped first time in winter 1992/1993 and second time in the autumn 2002. The mapping was done on the basis of field charts (1:500) of a stem position map including all trees>29 cm dbh (for map type please see Emborg et al. 1996). Phases were defined by the uppermost canopy layer of the patch. As an example, regeneration on the forest floor was only defined as an innovation phase patch in case there was a gap above, and trees between 3 and 25 m height were only defined as an aggradation phase patch if they formed the uppermost canopy layer of the patch. The advantage of this mapping method is that there can be no spatial overlap between neighbouring patches. The spatial resolution corresponded to a minimum patch size of 100 m². Clinometer, a caliper and measuring tapes were used to ensure a strict use of the phase definition. Each patch of the mosaic was marked on the field charts, digitised and the area of each patch was computed.

For the spatial analyses ArcGIS was used.

5.3 Results

The two maps of the results from the inventory in 1992 and 2002 are presented in figure 5.3 and 5.4. The main changes in area (see also figure 5.5) can be summarized in folllowing bullets:

1. The area of innovation phase significantly increased from 0.24 ha in 1992 to 0.80 ha in 2002, as a direct effect of the 1999-storm.

2. The area of late biostatic phase and degradation phase decreased.

3. The area of aggradation phase was rather stable and is very close to the area which could be expected from the model.

4. The only phase, which covers an area significantly larger than expected, is early biostatic phase.

---

Figure 5.3 - Model of the forest cycle of Suserup Skov. The phases are defined by measurable criteria, as indicated in the boxes. Usually climax microsuccession from Fraxinus excelsior to Fagus sylvatica occurs during the innovation, the aggradation and the early biostatic phases (From Emborg et al 2000)

Figure 5.3 - Forest development phases 1992, The squares represent the permanent plots (see chapter 4).

Figure 5.4 - Forest development phases 2002, The squares represent the permanent plots (see chapter 4).

Figure 5.5 - Changes in summarized area (ha) of phases from 1992 to 2002.
5.4 Discussion

5.4.1 The forest cycle
Based on the first survey of Suserup in 1992 a simple model of the forest cycle was launched (Emborg et al. 2000). The remapping in 2002 added much of new information to the understanding of the forest ecosystem in Suserup Skov. It is clear that the simple model (figure 5.1 and 5.2) explains a large part of the scenarios in the forest. However more processes take place and drive a particular spot in the forest in an, from a model point of view, unexpected direction. Some of the major driving forces are described in the following text, but information from chapter 3, 4, 6 and 7 must also be included in the understanding of this complex system. Even more processes probably influence the forest, by both external and internal factors. Some of the processes work fast, like a storm or dutch elm disease and others work very slow like general growth and competition among species.

5.4.2 Main driving forces in the forest ecosystem

The overall forest cycle
An evaluation of the forest cycle model from Emborg et al. (2000) can be summarised in the following supports and exceptions:

The model is supported by:
- The major part (50.9 percent) of the area of innovation phase in 1992 changed into aggradation phase in 2002.
- The major part (42.3 percent) of the aggradation phase in 1992 changed into early biostatic phase in 2002.
- The major part (57.3 percent) of the degradation phase in 2002 originate in areas of late biostatic phase in 1992.

Major exceptions:
- The changes between early biostatic and late biostatic run both ways
- Often the areas turn directly from late biostatic phase into aggradation og early biostatic phase.
- Many shortcuts exist, mainly due to different kinds of disturbance.

Dutch elm disease
Dutch elm decease arrived to Suserup in 1995 and has spread quite rapidly since. However almost only trees larger than 10 cm dbh are attacked and even in 2002 wych elm is the most frequent tree in the forest.
The disease causes suddenly dieback of young elm stands in aggradation phase and the early biostatic phase. Most often, areas attacked by dutch elm disease return to an innovation phase, which differ from the storm-initiated innovation phase by the lack of large lying dead wood and soil disturbance by uprooted trees. What kind of differences in the regeneration patterns this deviation leads to are not seen yet, due to the recent arrival of the disease.

Gale damage
3rd December 1999 Suserup was hit by a heavy storm (see chapter 6). The direct disturbance caused by this type of extreme wind speed differs significant from the normal small-scale disturbance. The latter is often caused by a combination of fungal attack, age and wind. In contrast a gale also hit trees, which are not significantly weakened by other causes and this often lead to uprooting and major destruction of the understorey.
It seems that storm damages are the most frequent initiators of the innovation phase.
The storm simply erases the degradation phase

Figure 5.6 - Changes in percent of total area (10.6 ha) from 1992 to 2002.

Figure 5.7 - Major effect of the storm in red colours. Major effect of dutch elm disease is indicated by violet colours
from the cycle and make larger gaps which provide favourable conditions for seedlings and regeneration establishment.

**Expansion of neighbouring crowns**
A non-neglectable process, which leads to change in the area of phases, is the process of expanding crowns in neighbouring phases. Areas of early biostatic phase where the trees finish their height competition and are able to allocate more recourses into horizontal expansion are the most aggressively expanding. Most vulnerable to this expansion are areas in the innovation phase. Often, small gaps with a patch of innovation in an area of early biostatic phase are simply closed by the surrounding trees, but also larger areas of innovation are normally significantly reduced in size by expanding crowns from neighbouring areas.

Beech and wych elm have good abilities of rapid horizontal expansion whereas ash seems to respond less effectively.

![Figure 5.8 - Changes in innovation phase.](image)

**Gradual takeover from understory**
Some areas seem not to follow the system of the cyclic development at all. Most obvios are cases where oak dominates the upper-canopy, with a vital understory of wych elm, beech and ash. When an oak dies or looses major branches it normally happens without major destruction of the sub-canopy. Gradually the trees in the under-story or sub-canopy takeover and the area in the sense of phases will step back to aggradation or early biostatic phase. The same patterns can be found where large ash dominated the upper-canopy, where as areas of large beech generally tends to follow the large cycle.
6 Storm damage

Jaris Bigler

6.1 Introduction

6.1.1 The goals of this study
A gale is a naturally occurring disturbance in Denmark and can be considered an integrated part of forest dynamics (White 1979). The gale results in varying degrees of damage to the standing trees and leads furthermore to creation of special features such as soil disturbance, creation of canopy gaps and accumulation of different types of coarse woody debris. These features are considered vital for the recovery of the forest system and the maintaining of high biodiversity. By documenting the structural impact of a severe gale on a natural mixed deciduous forest, it is possible to:

1) provide basic knowledge about the natural disturbance regime useable in the development of nature-based forest management as well as nature conservation,
2) provide a platform on which future research of the recovery of the system could be based, and
3) enable future comparisons of susceptibility of a natural mixed deciduous forest and even-aged monoculture stands.

On the 3’rd of December 1999 a severe gale hit Denmark and caused wide spread damage in forests and provided an opportunity to study the effects of gale disturbance in Suserup Skov. The results of this investigation are presented in this report.

6.1.2 Hypotheses and selected topics
In general, the severity of gale disturbance depends primarily on the velocity of the wind, but the impact on a forest is additionally influenced by many other factors (Helles 1983, Pontailler et al. 1997, Gardiner and Quine 2000). These factors work on different organisation levels:

1) On the single-tree level the species and size of the tree plays an important role for the rate and type of damage.
2) On the tree-group level, damage by other falling trees and local forest structure alter the species and size response.
3) On the forest part level, variations in the edaphic conditions is correlated to the distribution of damage types and differences in stand exposure can influence the over all damage rate.
4) On the landscape level, whether the trees are with or without their leaves is an important factor in deciduous forests and meteorological features such as precipitation and temperature can influence the damage rate of entire countries.

Since only the results from one forest are presented here, no conclusions about the factors working on this level can be drawn.

The contribution to the structural changes of a non-intervention forest of each of the factors listed from 1) to 3) above are analysed in this chapter, while testing the following three hypotheses:

1) Species and size of the tree are significantly correlated to damage rate and type.
2) Damage by other falling trees and the local forest structure alter the species and size response significantly.
3) Wet soil conditions and increased exposure lead to a higher damage rate.

Special topics directly resulting from the impact of the gale were selected for detailed investigation. These were:

a) the soil disturbance caused by the turnover of the root mats,
b) the creation of canopy gaps and
c) the accumulation of different types of coarse woody debris.

The role of forest structure and composition for development of these structures are analysed, the qualitative and quantitative data of these features are presented and the influence on habitat and species-diversity are discussed.
6.2 Materials and methods

6.2.1 The gale
The gale on the 3rd of December 1999 was a midlatitude cyclone. The strongest gusts (3 seconds means) at Flakkebjerg meteorological station (55°19' N, 11°23' E) on an exposed location 13 km southwest of Suserup Skov were of 45.1 m/s, and the highest 10-minute mean was 27.1 m/s (Danmarks Meteorologiske Institut 1999). The gale was the strongest ever recorded in Denmark, with gusts exceeding 50 m/s at the exposed Rømø island west of Jutland. The gale was passing fast with a duration of less than eight hours above level 10 on the Beaufort scale. The precipitation in the month before the gale was less than normal: 15 mm of rain against the normal 60 mm precipitation in for November in the southern and western part of Zealand (Cappelen and Jørgensen 2000).

6.2.2 Directly observed variables
All trees damaged during the gale with a DBH exceeding 15 cm were recorded and the following data collected: DBH (taken crosswise by callipers for trees smaller than 100 cm DBH and the circumference by measuring tape for trees greater than 100 cm DBH). The position of the tree was noted on a map along with the orientation of the debris (based on the 50 times 50 meter grid previously constructed). The status of the tree (whether the tree was dead or alive at the time of the gale incident) was noted. The cause of fall was judged from the marks on the damaged trees and from the sequence of the fallen logs and two categories were subsequently constructed: 1) Direct wind damage or 2) indirectly damaged by another falling tree. Furthermore, the species and DBH of the damage-maker were also noted in the case of damage by another tree. Additional data were collected depending on damage type, see Table 6.1.

We used the number of trees that were in the 14-19 cm class in the 1992-survey as an estimate for the number of standing trees which were 15-20 cm just before gale and so on, assuming an increment of 1 cm between the two surveys. More exact models of yearly increment are quite complicated to construct and might, apart from the size and age of the individual tree in the last survey, include corrections for climate, soil and competition (Emborg 1996) and are beyond the limits of this project.

If a tree had fallen, the disturbed soil was recorded. Mound height, mound thickness, mound diameter and tree length were measured by measuring tape. The type of the deepest lying soil horizon exposed by the falling tree was assessed using the guidelines of FAO-UNESCO (1990) and divisions were only made between an A-horizon, a B/E-horizon and a C-horizon. The A-horizon is characterised by a dark colour resulting from the mixture of organic matter and the mineral soil, the C-horizon by mineral soil not disturbed by the weathering processes and the B/E horizon is placed in between the A and C.

Trees where the roots were broken at the basis of the stem were classified as snapped trees. The area of a gap was defined as the surface delimited by the vertical projection of the edges of surrounding crowns (Runkle 1990, Pontailler et al. 1997). Maps showing the horizontal extension of the gaps were constructed based on field observations. The gaps were cut from the map and weighed on a Mettler scale (type H5, 1 div. = 10 mg) and the weights used to calculate their size.

6.2.3 Definitions
All changes in the structure of individual trees are categorized as “damage” even the term does not refer to an economic or biological evaluation of the change in structure.

Table 6.1 – Additional collected data. The first column divides the damaged trees into two groups depending on whether the point of fracture was at the roots or at an above-ground part of the tree. The next column shows the four fundamental types of damage and the last column is the additional data collected.

<table>
<thead>
<tr>
<th>Category</th>
<th>Damage type</th>
<th>Additional data collected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uprooted trees</td>
<td>Fallen (trunk parallel to forest floor)</td>
<td>Fall direction, Length of tree, Fall type (rotational or hinge), Deepest horizon made visible, Deepest point in pit, Diameter of mound, Height of mound, Thickness of mound</td>
</tr>
<tr>
<td></td>
<td>Fallen (trunk parallel to forest floor)</td>
<td>Angle between forest floor and trunk mound</td>
</tr>
<tr>
<td>Broken trees (still standing)</td>
<td>Snapped (trunk broken)</td>
<td>Height of breaking point</td>
</tr>
<tr>
<td></td>
<td>Branch loss (loss of major branch or crown part constitute more than 20%)</td>
<td>% Crown loss</td>
</tr>
</tbody>
</table>

Distinction was made between “rotational” and “hinge” fall types according to Beatty and Stone (1986). The rotational type is characterised by root breakage in the leeward side and the root ball is functioning as a ball bearing resulting in the mound placed inside the pit. The hinge type
is characterised by the leeward roots resisting breakage and functioning as a hinge and the mound is therefore placed outside the pit. “Uprooted trees” are the combined group of fallen and leaning trees. “Broken trees” are both the snapped trees and trees with branch loss. “Indirectly damaged trees” are damaged by the fall of another tree, and “Directly damaged trees” are damaged by the direct force of the wind. “Rooting depth” is defined as the thickness of the root plate and only measured on the fallen trees. “Mound height” is defined as the vertical distance from mound top to the bottom of the mound, mound diameter is the horizontal distance between the outermost parts of the mound where soil is intruded between the roots and mound thickness is the greatest distance in a right angle between the former forest floor and the exposed mineral soil at the other side. The horizontal “pit area” is defined as being equal to the above forest floor part of the vertical “mound area”. In a few cases no pit was created because the roots just turned below the soil surface but this was not broken. In these cases no pit area or mound volume were attainable.

6.2.4 Derived variables
The vertical area of the mound was calculated as half an ellipse based on mound diameter and mound height. In the case of hinge fall type, the root mat volume was calculated as a half cylinder assuming that the complete root plate is of an equal thickness (Beatty and Stone 1986). In the case of rotational fall type the root mat volume was calculated as one quarter of an ellipsoid because the shape of the root mat resembled more a rounded ball than a plate. The root plates created by the simultaneous fall of more than one individual with DBHs exceeding 15 centimeter were left out of the calculations of average sizes. The reason for this was because it was difficult to divide the common root plate into fragments originating from each of the different trees. When calculating the total area and volume, these collective root plates as well as the ones resulting from the fall of standing dead trees were included in the calculations. The standing snag volume was calculated as the cylinder, based on BA, times the height to breaking point. The standing snag volume of trees with a 100 % crown loss were calculated as 2/3 of the cone based on the height of the tree from the relevant height/diameter-regression, see below. The standing volume (SV) of damaged trees was computed per diameter class for ash, beech, oak and the rest of the species pooled, using the following equation:

\[ SV = \frac{1}{2} \pi DBH^2 h \]

The basal area (BA) was found for each DBH-class. The height (h) was found using a graphically height/DBH-relation for oak and individual height/DBH-regressions (hi = a* (DBH/ (DBHi + b))3 +1.3) for beech, ash and “other species”, all derived by Emborg et al. (1996). A form factor was derived from the Danish standard volume functions (Madsen 1987).

6.2.5 Statistical analyses
All trees with a diameter at breast height larger than 15 cm (dead as well as alive) were classified into the damage type categories as

\[ y_i(x) = \begin{cases} 1 & \text{if damage type } x \\ 0 & \text{otherwise} \end{cases} \] (1)

where \( N \) is the total number of trees in the forest. Assuming that \( y_i(x) \sim Bernoulli(p_i(x)) \) and that \( p_i(x) \) only depends on site, species, DBH and remains \( p_i(x) \) constant within combinations of tree species and sites, it follows that

\[ \sum_{j=1}^{N} y_j(x) \]

is binomially distributed \( Bin(N, p_j(x)) \). Furthermore, the sum

\[ \sum_{j=1}^{N} y_j(x) \]

equals the number of damaged trees of damage type \( x \) in the forest. It follows that we can use logistic regression analysis to address questions regarding the dependency of damage types on species, site and diameter. This type of analysis can be used to address questions such as whether oak suffers more from a certain type of damage than beech and, say, whether tree diameter affects the risk of damage. The analyses were carried out using the model

\[ \text{logit} \gamma_{i,j}(x) = a_i + \beta_i \cdot DBH_{i,j} \quad \forall x, \] (2)
where
\[
\text{logit } y_{ij}(x) = \log \left( \frac{y_{ij}(x)}{1 - y_{ij}(x)} \right),
\]
the index \(i(j)\) refers to individual \(j\) of the \(i\)’th species, \(\alpha_i\) corresponds to a species-specific intercept and \(\beta_i\) to a species-specific slope. Put simple, this model implies that we for each species model a separate straight line (one intercept and one regression coefficient for each species) of the logit to \(y_{ij}(x)\). The testing procedure of parameters \(\alpha_i\) and \(\beta_i\) is as follows. First we tested whether the set of species specific regressions could be adequately described with one common slope, i.e. we tested whether \(\beta_i = \beta\) for \(i = 1, 2, \ldots\). Second we tested whether the regressions could be assumed to have the one common intercept. i.e. if \(\alpha_i = \alpha\) for \(i = 1, 2, \ldots\). Note, however, if we reject the first hypothesis the second test makes little sense: Rejection the first and accepting the second hypothesis implies one regression for each species, each with different slope but all with the same intercept. In the case of acceptance of the first hypothesis we proceeded testing whether \(\beta = 0\). All the logistic regression analyses were carried out using SAS proc genmod (SAS, 1996).

Due to limitations in the data set, not all tests could be performed at all sites or for all species: not all species were represented at all sites and some species only suffered a limited array of damage types. For each analysis performed it will appear which sites and which species are included.

### 6.3 Factors influencing the amount and type of tree damage

#### 6.3.1 Results

In the entire Suserup forest 421 trees were damaged (see table 6.2), representing a BA (basal area) of 21.1 m². 194 trees were fallen (BA 40.7 m²), 72 leaning (BA 4.6 m²), 19 snapped (BA 34.8 m²) and 35 suffered crown loss (BA 21.5 m²). These numbers cover great variances with respect to species, size and spatial distribution, and these details are analysed further below.

Three main factors were identified and tested using the SAS GENMOD-procedure, see table 6.2.

<table>
<thead>
<tr>
<th>Source</th>
<th>Degrees of Freedom</th>
<th>(\chi^2)-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>5</td>
<td>36.94</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Size</td>
<td>1</td>
<td>87.32</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>96.32</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

All three factors significantly influenced the chance of damage of the single tree. However, all three factors interact intimately and this is described in detail below. Two more factors, only possible to describe indirectly, are the niche of the tree with respect to under-storey or dominant position in the system and the related role in the shifting mosaic of developmental phases.

The five factors determining the impact of a gale on a forest stand are structured according to their respective organisation levels. Starting on the singletree level and ending on the forest part level, working hypotheses were formulated and tested for each of the factors that are included in this chapter.

### Table 6.2 – Main parameters determining the chance of damage (all four damage types pooled). DBH was used as an indicator of size.

<table>
<thead>
<tr>
<th>Source</th>
<th>Degrees of Freedom</th>
<th>(\chi^2)-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>5</td>
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<td>Size</td>
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</tr>
<tr>
<td>Site</td>
<td>2</td>
<td>96.32</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

#### Table 6.3 – Damage rate and mean DBH of main species of Suserup. The rest consists of one fallen horse-chestnut (Aesculus hippocastanum), one fallen birch (Betula pendula), one fallen and one leaning cherry (Prunus avium) and one fallen mountain ash (Sorbus aucuparia). The damage rate differed highly significantly among species, see table 6.2.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of pre gale individuals &gt; 14 cm DBH</th>
<th>Number of individuals damaged</th>
<th>Damage rate</th>
<th>Mean DBH of pre gale individuals &gt; 14 cm DBH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beech</td>
<td>2492</td>
<td>235</td>
<td>9.4</td>
<td>33.9</td>
</tr>
<tr>
<td>Elm</td>
<td>1198</td>
<td>63</td>
<td>5.3</td>
<td>19.9</td>
</tr>
<tr>
<td>Ash</td>
<td>1035</td>
<td>70</td>
<td>6.8</td>
<td>32.1</td>
</tr>
<tr>
<td>Alder</td>
<td>444</td>
<td>0</td>
<td>0.0</td>
<td>32.8</td>
</tr>
<tr>
<td>Oak</td>
<td>181</td>
<td>15</td>
<td>8.3</td>
<td>96.5</td>
</tr>
<tr>
<td>Maple</td>
<td>156</td>
<td>23</td>
<td>14.7</td>
<td>23.9</td>
</tr>
<tr>
<td>Lime</td>
<td>48</td>
<td>10</td>
<td>20.8</td>
<td>30.3</td>
</tr>
<tr>
<td>Rest</td>
<td>208</td>
<td>5</td>
<td>2.4</td>
<td>19.9</td>
</tr>
<tr>
<td>All</td>
<td>5762</td>
<td>421</td>
<td>7.3</td>
<td>30.4</td>
</tr>
</tbody>
</table>
6.3.2 Single tree level
On the single tree level we tested the role of the species and the role of size for the rate and type of damage that were likely to occur to an individual tree. The characteristics of the main species in terms of damage type pattern and the size distribution among damage types are described in the following.

Species response
The seven most abundant forest tree species with a DBH greater than 14 centimetres prior to the gale were: beech, wych elm, ash, alder, oak, sycamore maple and broad-leaved lime (see table 6.3). To test whether the weak point is the root anchorage or the tensile strength of the wood, the categories fallen and leaning trees are summed to Uprooted trees and the trees with broken trunk and broken main branch are summed to Broken trees. The species could be sorted into two groups. The first group consists of wych elm, beech and broad-leaved lime that seems to have the weakest root anchorage; all three species have an uprooting percentage around 70. The second group consists of sycamore maple and oak that seem to be more fragile in the above ground tissue and structures. Ash is placed right between these two groups. Fisher’s Exact Test was used to separate frequencies of the two main groups, and they were just significantly different on the 5-% level. Beech and sycamore maple was used to the test ($\chi^2 = 3.9$, df = 1, p = 0.049).

The difference among species in their damage type distribution was significant ($\chi^2 = 52.97$, df = 18, p < 0.0001).

The type of damage suffered by the different species is presented in figure 6.1.

Damage and size
The mean DBH (all species) of the different damage-types were tested (one-sided ANOVA) as shown in table 6.4. The larger trees suffer dominantly from crown loss and the smaller trees end up leaning.

Table 6.4 – Mean DBH of the four damage types. The letters a, b and c label significant different mean DBH values (GLM-procedure, p < 0.001). The p-value of the two mean DBH values labelled b was 0.1454.

<table>
<thead>
<tr>
<th>Damage type</th>
<th>Mean DBH [cm]</th>
<th>Standard deviation</th>
<th>Range [cm]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaning</td>
<td>26.8</td>
<td>3.7</td>
<td>15-68</td>
</tr>
<tr>
<td>Fallen</td>
<td>42.5</td>
<td>2.6</td>
<td>15-144</td>
</tr>
<tr>
<td>Broken trunk</td>
<td>47.8</td>
<td>2.9</td>
<td>15-204</td>
</tr>
<tr>
<td>Broken Branch</td>
<td>84.7</td>
<td>5.3</td>
<td>24-132</td>
</tr>
</tbody>
</table>

Species, size and damage
The importance of the variables size, species and size*species were tested for each damage type using the GENMOD-procedure including the survivors of the pre gale population as a response. Six tests where chosen and are presented in table 6.5.

In general the correlation between the parameters “species”, “size”, “size*species” and the response seems better in part A than in part B.

In no cases was the “species” parameter significant on the 5 % level, but since the “size*species” parameter was significant in three cases in part A, the species included in those tests did perform different responses.

Only the damage-type “Fallen” seems to be non-significant regarding “size*species”.

6.3.3 Multi tree level
Widening the perspective from the singletree level to including the local structure and characteristics of nearby trees as factors, we can describe how the damage by other falling trees might alter the species and size response and explain some of the characteristics found in the species and size analyses. The local forest structure is included as a factor in the analysis, and its role for the multi tree episodes is evaluated.

Direct or indirect damage
The direct force of the wind damaged 245 trees and 164 trees were damaged due to the fall of another tree (indirect damage), equalling 0.67 indirectly damaged tree for each directly damaged. In the case of 12 trees, the cause of damage was not attainable.

The over all mean DBH of the indirectly damaged trees is only 44 % of the DBH of the
trees damaged directly by wind (see table 6.6). The mean DBH is even greater when looking only at the trees, which actually caused damage to other trees by their own fall; the average damage-causing tree is 41% larger than the average tree damaged directly by wind and 217% larger than the average indirectly damaged tree. 11 individuals were classified as damaged both directly and indirectly. The mean DBH of those trees was 46.9 cm, not surprisingly between the mean DBH of the indirectly and directly damaged trees. In six cases, a tree was damaged by the simultaneous fall of two trees, and both of those trees figure in the calculations as damage causing trees. All of these mean DBH-values were highly significantly different (t-tests, all p-values <0.001).

Of the trees where the cause of damage could be determined, 61.3% (38 out of 62) of the wych elm trees, 39.7% (93 out of 234) of the beech trees and 29.4% (20 out of 68) of the ash trees were damaged by the fall of another tree.

In general, the trees causing damage to other trees did hit 2.3 other trees, and 53% of the damaging trees did hit two or more trees (see table 6.7).

### Table 6.5a - Fallen, site A - only ash, beech and elm.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>$\chi^2$-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>2</td>
<td>5.22</td>
<td>0.0735</td>
</tr>
<tr>
<td>DBH</td>
<td>1</td>
<td>24.45</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Species*DBH</td>
<td>2</td>
<td>1.69</td>
<td>0.4290</td>
</tr>
</tbody>
</table>

### Table 6.5b - Leaning, site A - only ash, beech and elm.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>$\chi^2$-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>2</td>
<td>2.05</td>
<td>0.3588</td>
</tr>
<tr>
<td>DBH</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Species*DBH</td>
<td>2</td>
<td>6.49</td>
<td>0.0390</td>
</tr>
</tbody>
</table>

### Table 6.5c - Leaning, site B - only ash, beech and elm.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>$\chi^2$-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>2</td>
<td>1.90</td>
<td>0.3869</td>
</tr>
<tr>
<td>DBH</td>
<td>3</td>
<td>1.60</td>
<td>0.6599</td>
</tr>
<tr>
<td>Species*DBH</td>
<td>2</td>
<td>0.57</td>
<td>0.7527</td>
</tr>
</tbody>
</table>

### Table 6.5d - Snapped, site A - all six species.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>$\chi^2$-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>4</td>
<td>8.62</td>
<td>0.0712</td>
</tr>
<tr>
<td>DBH</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Species*DBH</td>
<td>4</td>
<td>10.05</td>
<td>0.0396</td>
</tr>
</tbody>
</table>

### Table 6.5e - Broken branch, site A - only beech, lime and oak.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>$\chi^2$-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>2</td>
<td>5.57</td>
<td>0.0617</td>
</tr>
<tr>
<td>DBH</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Species*DBH</td>
<td>3</td>
<td>61.66</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

### Table 6.5f - Broken branch, site B - only beech, maple and oak.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>$\chi^2$-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>2</td>
<td>3.96</td>
<td>0.1383</td>
</tr>
<tr>
<td>DBH</td>
<td>3</td>
<td>3.13</td>
<td>0.3720</td>
</tr>
<tr>
<td>Species*DBH</td>
<td>2</td>
<td>3.13</td>
<td>0.2093</td>
</tr>
</tbody>
</table>

Damage and developmental phases

The five developmental phases as defined in Emborg et al. (2000): Innovation, aggradation, early biostatic, late biostatic and degradation, were analysed using only data from part A and focusing on the three dominant species: Beech, ash and wych elm.

The rate of indirectly caused damage in the 5 developmental phases was compared, as well as the susceptibility to gale damage in terms of numbers of damaged trees, damaged volume and created gap area.

The rate of indirect damages decreases for beech but increases for ash through the phases as shown in figure 6.2. The shift takes place between the early and the late biostatic phase where the proportion of indirect damages among beeches decreases from 53% to 31%.
the aggradation phase has by far the lowest losses (2.5 m³/ha). The degradation phase seems to be the most structurally stable phase in terms of gap area resulting from the gale.

Two young beech trees close to the borderline of the phase and one large dead beech caused the relatively high volume of damaged wood in the innovation phase. This, combined with the low area of this phase, results in the relatively high volume per hectare. The two small beech trees were also responsible for the fact that there was created new gap area at all in this phase.

6.3.4 Forest part level

The three parts of the forest differed with respect to exposure to the wind, edaphic conditions and species composition (Fritzbøger and Emborg 1996, Vejre and Emborg 1996). The overall damage rates were ranging from 1.7 % in part C to 10.2 % in part A.

To limit the influence of variation in species composition, only beech data is used in the tests of influence of wind and soil on the forest structure.

Wych elm (not shown in figure) is generally more susceptible to indirect damage than beech and ash. The proportion of the total number of damaged trees is divided into the different phases as shown in figure 6.3 for ash, beech and wych elm. Wych elm seems to get most severely damaged in the innovation phase, ash in the early biostatic and beech in the early and late biostatic phase. If the same figure is constructed based on BA instead, wych elm still has a maximum in the innovation phase but both ash and beech have maximums in the late biostatic phase. The maximums for both ash and beech are more extreme if BA is used as indicator instead of number of damaged trees.

In terms of total number of damaged individuals per hectare (all species) the aggradation phase was most severely hit and the innovation phase least severely hit (see table 6.8), but due to the definition of the innovation phase, only exceptionally trees with a DBH > 15 cm are present in the innovation phase. If the total lost volume per hectare is considered (sum of fallen, leaning and snapped trees) the late biostatic phase experiences the greatest losses (21.4 m³/ha) and the aggradation phase has by far the lowest losses (2.5 m³/ha). The degradation phase seems to be the most structurally stable phase in terms of gap area resulting from the gale.

Table 6.8 – Impact of the gale on the five phases. All fallen, leaning and broken trees are included, but not the trees suffering from crown loss, since they are expected to survive. Apart from the area of the five phases, the rest of part A (0.3 ha) were classified as mixed phases in the 1992 survey.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Area in the 1992-survey [ha]</th>
<th>Gap area [ha]</th>
<th>Gap area in % of phase area</th>
<th>Volume fallen, leaning or broken [m³/ha]</th>
<th>Number of damaged trees/ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>Innovation</td>
<td>0.2</td>
<td>0.008</td>
<td>4.1</td>
<td>128.6</td>
<td>20.0</td>
</tr>
<tr>
<td>Aggregation</td>
<td>2.3</td>
<td>0.512</td>
<td>22.3</td>
<td>24.7</td>
<td>38.3</td>
</tr>
<tr>
<td>Early biostatic</td>
<td>4</td>
<td>0.508</td>
<td>12.7</td>
<td>57.6</td>
<td>28.0</td>
</tr>
<tr>
<td>Late biostatic</td>
<td>3.3</td>
<td>0.583</td>
<td>17.7</td>
<td>214.4</td>
<td>29.7</td>
</tr>
<tr>
<td>Degradation</td>
<td>0.6</td>
<td>0.186</td>
<td>31.1</td>
<td>119.4</td>
<td>35.0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>10.4</strong></td>
<td><strong>1.797</strong></td>
<td><strong>16.8</strong></td>
<td><strong>102.1</strong></td>
<td><strong>30.2</strong></td>
</tr>
</tbody>
</table>
Three hypotheses have been tested:

a) The three parts of the forest experience the same damage rate (all damages pooled).

b) The amount of uprooting is the same in the three parts of the forest.

c) The rooting depth corrected for tree size is shallower at the moist C part than on the elevated parts A and B.

Test a: The damage rate (damaged individuals) varied significantly among sites. The beech in part A had a damage rate of 11.1 %, in the moist lakeside part C it was 4.2 % and in part B it was 4.3 % ($\chi^2 = 28.5$, df = 2, p<0.0001).

Test b: The amount of uprooting (fallen and leaning individuals and only individuals alive immediately before the gale) amounted to 66.3 % of all damages in part A, 50.7 % in part B and 61.9 % in part C and the rates were not significantly different ($\chi^2 = 5.8$, df = 2, P = 0.055).

Test c: To test whether there was any difference between the rooting depth-DBH-ratio of the tree sites, this ratio was found using only paired beech-data of DBH and rooting depth. The expected difference between part C and the more elevated parts was not found.

6.3.5 Discussion

The damage type and rate depended on tree size and species, and was correlated intimately with the actual phase of the cyclic dynamics of the forest, and the structure developed according to these dynamics.

Tree size and species response

The tests using GENMOD-procedure showed in general, a good correlation between size and likelihood for damage of most damage types. Furthermore, this response seems to be species dependent (table 6.5). Only the fallen trees were poorly correlated with species in part A. The stronger correlation of part A compared with part B might be due to the irregular DBH distribution in part B, caused by the higher rate of human interference (see chapter 6.2.1).

A gradient exists between species, which tended to break above ground and species more likely to suffer from failure in root anchorage. Whether the first group was characterised by deep rooting or fragile above ground structures (stems or branches) cannot be concluded from this study. But our specific placement of certain species in one or the other end of the scale can be supported by literature.

The higher rate of uprooting among beech and lime was also found in Draved (Bigler 2002), and in the case of Beech supported by Andersen (1954) and Allen (1992).

The loss of crown parts or major branches is known to be a typical damage for oak and also observed after the storms of 1931 and 1934 (Gandil 1932,1934) in Denmark and by Cutler et al. (1990) after the 1987 gale in Great Britain. In Suserup this effect was more pronounced than normal since the oaks are greater than average tree size (the DBH-distribution for oak is better described as being bell-shaped than as being a negative exponential distribution (Emborg et al. 1996)). And as found in this study the largest trees are the ones that suffered most from crown loss, as also found by Bigler (2002) in Draved. This also explains why no oak was leaning at all; this type of damage was most likely to occur among trees with a small DBH, since the larger trees would reach the forest floor due to their higher weight. The opposite pattern with a lot of leaning trees was observed for wych elm and might be explained by the steep negative DBH-distribution curve as described by Emborg et al. (1996). Alder was harmed surprisingly little and apart from the structural adaptation to wind exposure close to the lake, general deep rooting (Ødum 1980) and former coppice management although limited (Christensen et al. 1993) might explain this fact.

Direct or indirect damage

Mostly it was the larger trees, which caused damage to smaller trees. The mean DBH of the indirectly damaged trees was only 44 % of the mean DBH of the directly damaged ones. This notable difference was also found by Clinton and Baker (2000). They found the indirectly damaged trees having a mean DBH of 16.6 cm against 32.6 cm for the directly damaged ones.

Cyclic dynamics implies that beech takes over the dominance of the canopy from ash at a given site during the early biostatic phase either due to the shorter life duration of the ash (ash degenerates typically after 130 years, beech typically after 250 years in this system) or due to the ability of beech to grow through the canopies of the ash (Emborg et al. 2000). The decrease of the indirect damage rate of beech and the increase for ash through the phases (figure 6.2) illustrates this: As the beech finally overgrows the ash, the pattern changes, and
ash now suffers from the fall of dominant trees. Wych elm being a shade tolerant under storey specialist (Emborg et al. 1996) was represented in large numbers in the small DBH-classes, and this lead to the high indirect damage rate. This was partly due to the few large individuals exposed to direct wind and partly due to the abundance of small individuals in the under storey.

**Phases, structure and damage**

Gale induced damages often tend to represent a bell-shaped curve on the DBH-distribution, as found by Pontailler et al. (1997) in a study of Fontainebleau forest (France) where a peak is found at a DBH of 50-80 cm. This implies an increase in vulnerability with DBH followed by a decrease in the amount of damages among the largest DBH-classes. Andersen (1954) explains the increase in vulnerability with age by the increase in wind velocity with height above the ground and the more flexible stems of young trees. Pontailler et al. (1997) explains the peak by stating that the most damaged trees have just reached the canopy and at the same time still possess a rather high height/DBH-ratio. This ratio decreases with age resulting in fewer damages among older trees. Cutler et al. (1990) on the other hand finds no such susceptible height/DBH-ratio, but finds that older trees with a less dense crown (resulting in a reduced area exposed to the force of the wind) are harmed less by a gale compared to younger and more vital trees. The negative exponential size distribution was another factor, which decreased the number of damaged trees per ha among older trees. This peak is reflected in the number of individuals damaged per hectare as shown in figure 6.3, where first wych elm, then ash and at last beech show a maximum peak in the overall damage rate. This is a result of the cyclic structure of Suserup Skov where the three species in the same order took over the dominance of the site after one another. Table 8 demonstrates the volume build-up through the phases: The late biostatic phase experiences the greatest losses in terms of volume, and the aggradation phase experiences the lowest losses even it had the highest number of damaged individuals per hectare. The structural stability of the early biostatic phase is interesting from an economic point of view, due to the high value of the standing volume in this phase. The created gap area is at a minimum at this stage and the lost volume per hectare is quite low compared to the other phases. The loss of volume in the late biostatic and the degradation phase is to a large extent bound in (from an economic perspective) over mature trunks. The early biostatic phase might face greater exposure in a managed forest where the older phases are not present but whether this will lead to greater losses is not obvious. The increased general exposure might result in adaptation and this could reduce the losses after a gale.

**Damage pattern and site**

The three sites of Suserup differ with respect to edaphic factors (Vejre and Emborg 1996). This combined with differences in management history (Fritzboger and Emborg 1996) results in varying species composition. This might explain why expectations of a higher damage rate of the more humid and exposed part C compared to the more elevated parts were not met. In particular, the high amount of alder in part C reduces the amount of damage in this part of the forest. Everham III (1995) finds a similar lack of connection between site and damage rate in a literature study. Furthermore the trees at the exposed part C might compensate for the constant exposure to wind by more resistant structures (Quine 1988, Cutler et al. 1990). A higher proportion of uprooted trees out of total damaged was expected in part C, compared with part A and B, due to the more moist conditions here. The wet conditions are known to prevent vertical root development and reduce the tension strength of the soil (Quine et al. 1995), and shallow root development is known to result in increased rate of fallen trees (Andersen 1954). Neither a higher rate of fallen trees or a shallower root development was found. The reason might be a poor correlation of the arbitrary defined site borders (the accuracy is limited due to the 50x50 meters grid on which the extent of the three forest parts are based) and the actual edaphic conditions.

**6.3.6 Conclusion**

The species and size of trees are important factors in determining the probability of damage, as well as the type of damage to the single tree in the forest. The domino effect of further damages caused by larger falling trees cause additional damage mainly to smaller trees, particularly among shade tolerant species growing in the sub canopy strata.

The adaptation of structure (on stand as well as
on single tree level) and species composition to the site seems to compensate for differences in exposure and edaphic conditions. Exposed and wet soil conditions do not necessarily lead to a higher damage rate. It was not possible to determine whether it was the structural adaptation or the fact that the species composition was suitable for the site, that was the most important factor resulting in the damage rate being lower than expected.

6.4 Coarse woody debris

6.4.1 Results

The total volume of lying CWD were ranged from 23.2 m³/ha in part C to 75.9 m³/ha in part A and the total volume of leaning trees from 1.7 m³/ha in part B and C to 4.1 m³/ha in part A (table 6.9). Beech dominated the volume, but the distribution among species varied with the species composition on the different sites. In the entire forest 112 broken trees resulted in 94 snags above a height of 0.5 metres (table 6.9). The mean standing snag volume was 8.5 m³/ha of which approximately 65% was beech, 20% oak and 15% ash. The mean size was 1.7 m³, but 6.6 m³ for oak.

All the created snags and all the fallen trunks of oak were larger than 80 cm DBH. The same numbers for beech were 21% for each types of CWD and for ash 18% and 4% respectively. None of the other species reached this size.

6.4.2 Discussion

Quantitative data from Suserup compared with literature

Compared to the provisional benchmarks for dead wood in British forests, where 0-10 standing snags per hectare is categorised as “low” and similar to the values found in managed forests (Kirby et al. 1998), the 4.9 snags per hectare seem rather low. But when comparing the numbers of Suserup with the British benchmarks the number of snags already standing in the Suserup has to be added to the numbers created by the gale. However, the over all conclusions are that typically snags are created during the normal conditions by the slow decay of the standing trees and not especially due to gales (Barden 1981).

The British values for fallen dead wood seem on the other hand to indicate that abundant resources of this particular type of CWD were created: More than 40 m³/ha is considered a high volume and in part A the mean volume was 57 m³. Kirby et al. (1998) which find that the amount of CWD is doubled by a gale and Van Den Berge et al. (1993) find the amount of CWD rising four times, so the total amount of CWD in Suserup might be considerable higher. The provisional British benchmarks are on the other hand quite low compared to the list of fallen dead wood in old-growth temperate deciduous forests also presented in Kirby et al. (1998), ranging from 46 m³/ha to 132 m³/ha with data from 13 different forests. Only part A, that is the least disturbed site, is surely within the range of other old-growth temperate deciduous forests.

The quality of the CWD

Apart from quantitative features the quality of the CWD is important when the impact on biodiversity is evaluated. Qualitative features are size distribution, spatial distribution and species composition.

In general, a larger diameter of logs is preferable for many organisms (Samuelsson et al. 1994). This demand is met by beech and oak, both species having individuals, which dominate the canopy for centuries. The calculation of volume of such large trees is quite uncertain due to the lack of reliable tables, but each trunk represents a considerable volume and constitutes a valuable niche for many communities of different organisms.

Spatial distribution is another qualitative parameter worth noting. Snag density requirements are best met by providing snags in dispersed clumps rather than as single trees.

Table 6.9 – Three types of dead wood resulting from the gale: Standing snags, trees lying on the ground and trees leaning in other trees. The category “Rest of snapped trees” covers the trees broken beneath 0.5 m and the top parts from the snapped trees with a standing snag higher than 0.5 m. Volume [m³ ha⁻¹] and (number ha⁻¹).

<table>
<thead>
<tr>
<th>Position of CWD</th>
<th>Origin</th>
<th>Part A</th>
<th>Part B</th>
<th>Part C</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lying</td>
<td>Rest of snapped trees</td>
<td>18.8 (0.6)</td>
<td>37.9 (2.0)</td>
<td>10.0 (0.5)</td>
<td>22.0 (0.9)</td>
</tr>
<tr>
<td>Lying</td>
<td>Fallen</td>
<td>57.1 (13.5)</td>
<td>11.1 (3.3)</td>
<td>13.2 (2.7)</td>
<td>37.0 (8.8)</td>
</tr>
<tr>
<td>Leaning</td>
<td>Leaning</td>
<td>4.1 (5.8)</td>
<td>1.7 (1.6)</td>
<td>1.7 (0.3)</td>
<td>3.0 (3.7)</td>
</tr>
<tr>
<td>Standing</td>
<td>Standing snags &gt; 0.5 m height</td>
<td>9.4 (6.6)</td>
<td>10.8 (4.1)</td>
<td>2.9 (0.8)</td>
<td>8.5 (4.9)</td>
</tr>
<tr>
<td>Sum</td>
<td></td>
<td>89.3 (26.4)</td>
<td>61.5 (11.0)</td>
<td>27.8 (4.3)</td>
<td>70.5 (18.3)</td>
</tr>
</tbody>
</table>
uniformly scattered over an area (Samuelsson et al. 1994). The nature of gale damages with the concentration of damages in larger hot spots complies with this demand perfectly. Relatively few species dominates the forest composition, and the composition of species among the created CWD reflects this fact. Beech, ash and oak dominates the volumes, partly due to the large dimensions of beech and oak.

The role of CWD
It seems doubtful that decaying wood plays any important role for the regeneration of trees (by serving as “nurse logs”) in Suserup, even though mountain ash is reported by Falinski (1986) from Bialowieza in Poland to be able to use this strategy. But for plenty of other groups of organisms this resource plays a vital role.

6.4.3 Conclusion
The conclusion is that a major and valuable accumulation in the store of CWD was the result of the gale, but the most interesting part is perhaps the abundance in space and time more than the volume itself, since the volume would have ended up as CWD anyway.

6.5 Soil disturbance

6.5.1 Results
Quantitative parameters
All together 197 trees created mounds. In 11 cases the forest floor was elevated but not broken, and as a result no thickness was measured. In these last cases it was not possible to estimate the volume of the root mat. The most numerous species were beech (122 root mats produced equaling six per hectare), ash (n=26, ~1/ha) and wych elm (n=22, ~1/ha).

The largest volume turned over by a single tree was 28.8 m³ - a rotational fall of a beech, and the smallest rotational fall was an wych elm with a volume of only 0.0136 m³. The largest hinge fall mound volume was also a beech with a volume of 22.1 m³, and the smallest hinge fall was an ash with a volume of 0.00733 m³. The quantitative data per hectare is shown in table 6.10 and 6.11. The average mound volume after fallen living trees was 3.3 m³ (derived from 180 trees with a mean DBH of 41.1 cm) and the corresponding average mound after dead trees was only 0.98 m³ (derived from six trees with a mean DBH of 75.0 cm).

Two types of regressions were made between biomass and the amount of soil disturbance, using all paired data of beech only. DBH was used as a parameter of biomass and this was correlated with vertical root plate area and root plate volume. The relationship between DBH and pit area resulting from a rotational fall did resemble a linear regression

$$\text{pit-area}_{\text{beech}} = 0.33 \times DBH_i - 4.32, R^2 = 0.83$$

The same relationship was not attainable for the hinge fall type due to the low number of data. The hypothesis was that the moister conditions at part C should result in a root plate with a greater horizontal extension, but no significant difference was found between part A and part C. The DBH were correlated with the volume of the root mats (figure 6.4) of the hinge falls

$$\text{mound-volume}_{\text{beech}} = 0.0349 \times DBH_i^{2.0271}, R^2 = 0.26$$

and rotational falls

$$\text{mound-volume}_{\text{beech}} = 0.001 \times DBH_i^{1.0777}, R^2 = 0.70$$

Table 6.10 – Mound volume [m³ha⁻¹] and (number ha⁻¹).

<table>
<thead>
<tr>
<th>Site</th>
<th>Part A</th>
<th>Part B</th>
<th>Part C</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>R-type</td>
<td>44.7 (12.8)</td>
<td>4.2 (3.1)</td>
<td>5.8 (1.6)</td>
<td>26.9 (8.2)</td>
</tr>
<tr>
<td>H-type</td>
<td>3.5 (1.0)</td>
<td>1.0 (1.2)</td>
<td>0.0 (0.0)</td>
<td>2.2 (0.9)</td>
</tr>
<tr>
<td>Sum</td>
<td>48.2 (13.8)</td>
<td>5.2 (4.3)</td>
<td>5.8 (1.6)</td>
<td>29.1 (9.1)</td>
</tr>
</tbody>
</table>

Table 6.11 – Pit area [m²ha⁻¹] and (number ha⁻¹).

<table>
<thead>
<tr>
<th>Site</th>
<th>Part A</th>
<th>Part B</th>
<th>Part C</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>R-type</td>
<td>119.8 (13.1)</td>
<td>14.6 (3.3)</td>
<td>12.9 (1.9)</td>
<td>77.4 (8.4)</td>
</tr>
<tr>
<td>H-type</td>
<td>14.0 (1.0)</td>
<td>6.3 (1.2)</td>
<td>7.4 (0.5)</td>
<td>10.8 (1.0)</td>
</tr>
<tr>
<td>Sum</td>
<td>133.8 (14.1)</td>
<td>20.9 (4.5)</td>
<td>20.3 (2.4)</td>
<td>88.2 (9.4)</td>
</tr>
</tbody>
</table>

Figure 6.4 – Correlation between mound volume and DBH of the two fall types: Rotational and hinge. Solely paired beech data, all sites pooled.
Using the entire data set, the mean root mat volume of the R-type significantly exceeded that of the H-type (\(F = 39.18, \text{df} = 1, P < 0.0001\)) even if the data were corrected for tree size (DBH) and species.

**Qualitative parameters**
All directions of fallen and leaning trees exhibited bell shaped curves around a peak at 38°. This resulted in 50% of the former forest floor sides of the root mats facing within 17° to each side and 90% to face within 50° to each side of the mean, and the same pattern around a mean value of 218° for the exposed mineral soil sides.

The deepest horizon exposed when a mound was created, was in 10.9% of the cases an A, in 62.1% it was a B and 27.0% it was a C-horizon (see Table 6.12).

<table>
<thead>
<tr>
<th>Table 6.12 – The share of the deepest horizons exposed on the mounds being an A-, B- or a C-horizon.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Part A</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>A</td>
</tr>
<tr>
<td>B</td>
</tr>
<tr>
<td>C</td>
</tr>
</tbody>
</table>

**6.5.2 Discussion**

**Mound size**
Large amounts of soil were turned over by large single trees, but the variation of mound size between individual trees was enormous. The largest mound was almost 4000 times larger than the smallest one. The larger mounds were generally created by the rotational fall of large beech trees, which were alive when the gale struck. In contrast, the mean mound volume of dead trees was much smaller than the mean mound created by a living tree, especially if corrections for DBH of the trees were made. This is supported by Lyford and MacLean (1966) and underline the importance of gale induced wind throw for the rejuvenation of the soil, since the weakly anchored dead trees are more representative of the falls usually occurring between two major gale events.

**Suserup compared to other soil types**
If the root plates radii are divided into four categories: <0.5m, 0.5-1.0m, 1-2m and >2m, the relative numbers of Suserup (all three sites pooled) are: 3%, 27%, 45% and 25%. Cutler *et al.* (1990) have comparable observations of 2%, 58%, 34% and 6% respectively, and corresponding data from Draved are: 0%, 4%, 47% and 49% (Bigler 2002). The data situates the root plate radii of Suserup right between the ones of the two other surveys. Since trees growing under wet conditions are known from literature (Mueller and Cline 1959) to increase the radius of the root plate at the expense of the rooting depth, it was expected that the rooting depths of Suserup were between the ones found in the other surveys. This was actually the case: 56% of the trees in the investigation of Cutler *et al.* (1990) have a root plate thickness of one meter or more where we find 21% in Suserup and Bigler (unpublished data) find less than 3% in Draved. Interestingly though, no difference in root plate area was found between the sites in Suserup.

**Two fall types with different qualities**
The rotational and the hinge fall type offer quite different micro sites since the hinge type results in a pit free of root mat and the entire soil volume displaced to the forest floor (Beatty and Stone 1986). This might be an important feature in a moister ecosystem where the mounds would assemble “islands” of dryer conditions in a “sea” of moist soil (Lyford and MacLean 1966, Beatty and Stone 1986). However the majority of Suserup forest is placed on well drained soils, and the hinge fall type was not abundant. The most important effect of the mound and pit creation in a forest like the elevated parts of Suserup is therefore the exposure of mineral soil and the rejuvenation of the soil as demonstrated by Lutz (1940), influencing the regeneration of the site. In general mounds seem to be an attractive spot for regeneration as found by Lyford and MacLean (1966) and Beatty and Stone (1986), eventhough the deposition of seeds seem to be lower (Clinton and Baker 2000). Lyford and MacLean (1966) find the mineral soil on newly created mounds to be a perfect seedbed for species like birch. The value of the soil turnover strengthens by the high percentage of deeper horizons exposed (table 6.12).

In part C and the few moist areas of part A and B, the variations in micro relief might play a significant role by inducing greater soil moisture gradients, but only few trees actually fell on such sites. However, smaller variations in soil moisture and temperature might still play a role in the rest of the forest. Lutz (1940), for example, finds the daily temperature amplitude to be more extreme on mounds than on the forest floor or in pits, Beatty and Stone (1986) find the same pattern of...
the yearly amplitude and Millikin and Bowden (1996) observe a general higher temperature on mounds compared to pits and forest floor while conducting soil respiration research. Clinton and Baker (2000) conclude that the variety of soil moisture and soil temperature induced by the mound formation exert a strong influence on the future forest composition.

Impact on biodiversity
The features characterizing recently created mounds favor pioneer species with typical characteristics such as high tolerance to frost and drought (Röhrig 1991). Not only the diversity of trees and scrubs is increased due to the turnover of soil. Schnitzler and Borlea (1998) find a temporary general increase in the diversity of shade intolerant species on soil held by roots in south facing gaps, and Jonsson and Esseen (1990) find twice the number of bryophyte species on wind disturbed sites and higher within plot diversity on those sites compared to the undisturbed forest floor.

Mounds: An integrated part of the forest ecosystem
We expect the structural diversity induced by the mound and pit formation to be long lasting due to the enormous size of the largest ones. From literature (Stephens 1956) mound and pit complexes are known to last up to 500 years resulting in a hummocky micro relief. Mueller and Cline (1959) find that most of a forest floor has been disturbed by mound creation within the previous 500 years. This should result in a forest floor almost entirely consisting of mound and pit complexes, suggesting the phenomenon to be a vital part of the forest ecosystem instead of a rare event. This is supported by Beatty (1984) who finds such strong preferences to the three types of micro sites (the unaffected forest floor, the mound and the pit) of different species, that she concludes that these features are an integrated part of the forest community.

The great chemical differences between the surfaces of the exposed mineral soil and the undisturbed forest floor will be diminished with time (Lyford and MacLean 1966, Beatty and Stone 1986), but the total effect is still an important renewal of the soil (Armson and Fessenden 1973, Bormann et al. 1995).

Homogenous fall directions
The direction of fall is the only feature that results in more homogenous conditions than would have appeared under the usually more calm disturbance regime with scattered uprooting resulting from wind from different directions. Almost all the mounds of Suserup are facing their mineral side to the southwest due to the dominating direction of the gale, with a normal distribution of up to 90° in each direction. As a contrast, Falinski (1976) finds the mounds created by smaller wind throws over a decade as showing a far greater diversity of fall directions. Cutler et al. (1990) find similar homogenous fall directions inside forests but more variable directions of solitary trees outside forests.

6.5.3 Conclusion
The creation of large long lasting mounds with exposed unweathered soil is the result of the forced turn over of living trees – a special feature of gale damage. The creation of mounds results in a greater variety of three important factors than before the gale struck: Moisture, temperature amplitude and substrate available for plant establishment. This results in an increase in the amount of special niches compared to the undisturbed forest. Only the fall directions limit the variability of niches compared to pre-gale conditions.

6.6 Gaps

6.6.1 Results
All together 49 gaps with a mean size of 450 m² were covering 20.4 % of part A immediately after the gale. Of these 49 gaps, four were considered to be old gaps (corresponding to 1.2 % of part A), three of which had expanded considerably during the gale. The total gap area was 14 times greater after the gale than prior to the gale. The gap size distribution (figure 6.5 and 6.6) shows an exponentially decreasing curve in terms of numbers but an increasing curve in terms of area. The largest gap was covering 0.45 ha. Only the two largest gaps have a gap-diameter/ surrounding-canopy-height-ratio of more than two (the limit above which full daylight is reaching the forest floor of the gap (Runkle 1985)), if the surrounding canopy height is assumed to be 30 meters.
6.6.2 Discussion

Gap size in Suserup compared to values from literature
The mean gap size of Suserup was 450 m², and compared to Pontailler et al. (1997) who find a mean gap size of 175 m² in a beech dominated forest in Fontainebleau (France) after a gale of similar magnitude, the perturbation in Suserup was severe. On the other hand, other authors report larger mean gap sizes from other deciduous temperate forests, for example Clinton and Baker (2000), but great differences in the allowed minimum size exists, and this will contribute greatly to the value of the mean size since the number of gaps increase exponentially with decreasing size. Pontailler et al. (1997) find a positive correlation between the mean gap area and the time passing between two storms, and that might also contribute to the different values in the literature.

Large gaps – a typical feature of gale disturbance
The creation of larger gaps is a typical feature of gale damage (Quine et al. 1999). One reason is that the large gap makers cause further destruction on their path towards the ground, which, at Suserup was reflected in the rather high rate of indirectly damaged trees (0.67 for each directly damaged) and the average number of 2.2 trees damaged by the fall of one of the damage-causing gap makers (table 6.7). If these damage-causing trees had died standing, occurrence of these extended damages would have been unlikely. This domino effect though, is only partly responsible for the gap extension. The other important factor is the increased structural roughness of the canopy layer once a hole is created. This causes the wind to become more turbulent and this will induce greater wind forces on the surrounding trees, which might eventually collapse under the increased stress (Allen 1992, Quine et al. 1995).

Gap closure
At very low values of the D/H-ratio the dominating gap closing dynamic will be lateral extension of the surrounding trees (Runkle 1990). The range of gap size where lateral closure will dominate depends on whether suppressed trees survive the collapse of the gap maker. If no harm is caused to a suppressed tree the further success depends on its starting height, its ability to respond with a release in the growth rate and on the competition of the lateral closure of the gap. If the suppressed trees are harmed, two resulting scenarios are possible: The trees could be snapped or wind thrown. In the first situation the snapped tree can resprout, and this is an especially common and temporary successful feature among wych elm in Suserup as described by Emborg et al. (2000). This is also the case if the gap maker itself is broken.

In large gaps, on the other hand, where most of the dominant and suppressed trees are wind thrown, the microclimate, the soil conditions and the seed sources available determine the composition of future species.

Micro climate in gaps
Runkle (1985) points out that the microclimate of the forest floor in a gap is dependent on the ratio between the gap-diameter and the height of the surrounding canopy, and that this has important implications for the future species composition. The available sun light at the center of the gap increases with the ratio and reaches maximum (full daylight) at a value of approximately 2, depending on features like latitude and topography. At Suserup, the two large multi tree gaps which are covering just less than half a hectare each, have the potential to lead to higher
species diversity by offering niches to earlier succession stages than the gaps created by the death of a single or few individuals (Whitmore 1989, Röhrig 1991), which is the normal gap dynamics between the strong gales (Quine et al. 1999).

Apart from the largest two gaps in Suserup, maximum solar radiation may also be possible in other gaps, due to variations in gap shape and surrounding canopy height.

**Regeneration strategies and biodiversity**

The result of this creation of larger gaps is a further displacement in the competitive relationship between the regeneration strategies towards new seeding at the cost of release of suppressed under-storey individuals (Runkle 1985). This means that larger gaps generally favour shade intolerant pioneer species and smaller gaps generally favor the climax species (Runkle 1985, Quine et al 1999, Clinton and Baker 2000). Röhrig (1991) states that only in larger gaps will heliophilous plants stand a chance. The success of the pioneer species in larger gaps is due to their abundant production of light seeds with a high tolerance to frost and drought and a fast juvenile growth rate (Röhrig 1991), however the seed banks of other species may alter the competition situation (Connell 1989).

The gap must be of such a size that the pioneer species can reach reproduction age before the gap is closed by horizontal growth from surrounding canopy trees, which survived a storm, to maintain the species in the system. Whitmore (1989) supports the importance of the gap phase for the following composition of the forest. Rapid colonisation and competition ability are trade-offs (White 1979), which, in the long run, will lead to a substitution of pioneer species with climax species without disturbance (Whitmore 1989). Gaps in general are supposed to lead to higher diversity, and the great heterogeneity of solar radiation in gaps in temperate regions results in a high number of different niches, maintaining high species diversity (Runkle 1989, Whitmore 1989). As an example Schnitzler and Borlea (1998), finds the high diversity among woody plants to be due to gaps in a mixed deciduous forest in eastern France, in agreement with White (1979) who finds that exclusion of disturbance lead to a drop in biodiversity.

This may not only leave habitats to the shade intolerant species with pioneer characteristics supposed to colonize immediately after gap formation, but may change the future species composition of the following cycle (Whitmore 1989), a hypothesis also proposed for Suserup by Vejre and Emborg (1996). Barden (1981) finds that these disturbances can maintain rare and shade intolerant species in the forest system. Furthermore Vejre and Emborg (1996) postulate that in the normal small gap dynamics of Suserup the patch size is too small to let the vegetation express the soil variation, but that this could be altered after a catastrophic event.

### 6.6.3 Conclusion

Gaps resulting from gale impact are larger than the ones occurring under calm conditions. The normal single-tree-gaps result in Suserup in a mosaic structure dominated by an ash-beech cycle. The larger gaps created after the 1999-gale might result in greater woody species diversity and are expected to favour especially the shade intolerant species. Other groups of organisms might additionally benefit from the change in microclimate.

### 6.7 Discussion

A strong gale like the one that passed over Denmark 3’rd of December 1999 results in serious perturbation to a non-intervention forest, but still no larger gaps than 0.45 ha occurred. The adaptation of structure and species composition to the site-specific exposure and edaphic conditions seems to secure the immediate resistance of the system, and a total collapse of the forest structure, as monitored in many even aged spruce-plantations, was not the result of the severe wind stress. The wet soil conditions and the increased exposure in the lakeside part of the forest did not lead to a higher damage rate.

The damage type and rate depended on tree size and species, and was correlated intimately with the actual phase of the cyclic dynamics of the forest. The damage caused by other falling trees primarily resulted in additional damage on smaller trees growing in the sub canopy strata. This in particular results in large amounts of additional damages among wych elm, due to the strategy as a sub canopy species and the high amount of young wych elm trees.

The major structural changes induced on the forest
system by the gale are the accumulation of dead wood, the disturbance of the soil and the creation of gaps. The abundance of CWD in space and time is seriously altered by the gale since the volume increased dramatically. The gaps created are larger than the ones occurring under normal disturbance regimes. The disturbance of the soil seems to be a vital and integrated part of the forest ecosystem resulting in a renewing of the soil.

All three types of structural changes are expected to have serious influence on the regeneration of the system and the maintaining of high biodiversity, due to the rise in structural diversity and creation of habitats important for specialized organisms. Many of the different microhabitats do not occur under the “normal” disturbance regime. Moreover, the extent of the creation of large gaps and the turnover and exposure of mineral soil as well as the creation of moist pits are only found in temperate deciduous forests after strong gales (Lyford and MacLean 1966, Quine et al. 1999).

The high diversity of micro sites is due to the large number of combinations of factors such as: Horizontal position in relation to especially the large gaps (differentiated light- and moisture regimes), geographical position in relationship to mounds (sun exposed south side or shaded north side) and variety in substrates (moist pits, mineral soil on the mounds, forest floor or decaying wood). Although some of the altered conditions listed are also available under normal disturbance regimes (for example decaying logs), the magnitude and severity of the changes can be drastically altered by the gale and, perhaps more important, the interaction with the new gale-induced features might lead to new patches available for specialists (for example sun exposed lying dead wood).

6.8 Perspectives

Whether or not the described increase in available habitats will result in higher species diversity or not, depends, among other variables, on the available seed sources. A pollen diagram (Hannon et al. 2000) from Suserup tells the story of a previous forest on the site much richer in species, and that the forest with few dominating species we see now is the result of anthropogenic clearance for agricultural purposes at approximately 600 BC. On the other hand species like broad-leaved lime (Emborg et al. 1996) has been reintroduced by humans and other new species like sycamore maple has arrived to the forest and are expected to expand further (Emborg et al. 1996). The result of the combined effect of gale induced structural change and the availability of seed sources of species, that until the gale struck were rare in the system, should be monitored in the years to come. Other groups of organisms might additionally benefit from the disturbance, and the documentation of the structural changes presented in this report might provide a platform for the research on the role of gale disturbance for the maintenance of high biodiversity in the forest system.
7 Re-measurement of the Silvistar plot

Anders Busse Nielsen and Katrine Hahn

7.1 Introduction

In this chapter, data from the re-measurement of the Silvistar plot in Suserup Skov will be presented and analyzed. The main questions asked were: How does Suserup Skov look beneath the uppermost canopy layer and how is the relative light intensity in the understorey related to the structural patterns and the vertical stratification? The permanent plot was measured in 1992 (Emborg, unpublished data) and re-measured in 2002 (see also chapter 2). The re-measurement enables a study of dynamics in vertical stratification and horizontal pattern on a singletree level.

7.2 Materials and methods

The plot is 120x80 m (0.96 hectare) orientated north to south (see figure 7.1). The terrain drops slightly (ca. 7 meters) from the north-west corner to the south and east. Two small footpaths run through the plot and a small forest bog is situated in the north-east part of the plot.

7.2.1 Setting a local co-ordinate system

A local co-ordinate system with permanent corner posts was laid out, dividing the plot into eight transects of 120x10 m. Each strip was again divided again into six parts of 20x10 m for handling of the mapping and drawings.

7.2.2 Tree charting

All trees >5 cm diameter breast height (dbh) were recorded on single-tree level according to the methodology described by Koop (1989). Horizontal characters were drawn on field charts while vertical and qualitative characters were recorded in tables. By giving each tree a unique number we linked horizontal, vertical, and qualitative data. Horizontal characters were drawn to scale 1:200 on millimetre paper sheets in the field. The characters charted were: tree positions, crown projections (based on 4 points), dead wood positions (fallen dead trees or branches >30 cm diameter, uprootings, standing dead trees, stumps from former forest management), and footpath positions. Crown projections for each tree were drawn using “imaginary vertical plans” parallel and right angled to the local grid (Koop 1989). The hand drawn chart and a comparison with the chart from 1992 served as the first control in checking for mistakes. Crown projections of each developmental phase were made manually using transparent sheet-overlay. The crown projections were scanned and adapted in Photoshop.

7.2.3 Tree measurements and classification

All vertical characters were recorded in tables on site. For each living tree with a dbh >5 cm, measurements of top height, height of the greatest width of the crown periphery, height of the crown base (defined as the lowest branch that is part
of the crown), and height of the first living fork (if under the crown base) were made, using a clinometer. Following the methods described by Koop (1989 p. 204-205) each living tree was classified in accordance to species, growth potential and damage. Furthermore, each living tree was given a social score in the form of a crown classification. Also characteristics of dead trees were recorded in the table.

7.2.4 Profile drawings
Hand drawn profile diagrams were made for two transects of each 10x120 m (transect number 2 and 4 from the western edge of the plot). Similar to the horizontal charting, each transect was divided into six sections of 10x20 m and depicted to scale 1:200. All trees within a section were drawn on the same sketch sheet. Tree charting and measurements were used as helpful points of support when drawing a tree. In order to keep the profile drawing readable, Koops (1989) method of “nested transect” was used for delimitation of the trees to be included in the profile. Trees of decreasing size was depicted in proportionally narrower strips: Trees over 10 m in height were drawn over the whole 10 m wide area (1200 m² each transect), those between 2 and 10 m were recorded over a 5 m wide area (600 m²) and those smaller than 2 m were recorded over a 2 m wide area (240 m²) around the center line. Both profiles are viewed from west. Using transparent overlay, the field sketches were transferred to one sheet, and scanned and adapted in Photoshop.

7.2.5 Mapping of developmental phases
The structural dynamics of the permanent plot were studied through a specific model of the forest cycle based on Emborg et al. (2000). In addition to the forest cycle described by Emborg et al. (2000), an extra phase was defined, by dividing the aggradation phase into two phases. Thus, six distinct phases were used: innovation (20 cm-3 m height), early aggradation (3-15 m height), late aggradation (15-25 m height), early biostatic (25 m height – 80 cm dbh), late biostatic (> 80 cm dbh), and degradation (degrading canopy – established regeneration). In this chapter the phases are related to a single tree level and not surface area as Emborg et al. 2000 (see chapter chapter 5).

7.2.6 Relative light intensity (RLI)
Along the centre line of the two transects depicted as profile drawings (transect number 2 and 4), the leaf area index (LAI) of the canopy was determined at 2 m intervals (60 points for each transect) by the use of the Li-Cor LAI2000 instrument. The measurements were carried out in the evening twilight at the 7th (transect 2) and the 12th of September (transect 4). Two simultaneous measurements were taken with the cross-calibrated sensors; one sensor was placed in the open and one sensor was used for measurements under the forest canopy (1 m above ground). The measures of LAI were converted to relative light intensity (photosynthetic photon flux densities) (PPFD) (µmol m² s⁻¹) in the 400-700 nm waveband, using a equation based on correlation tests of LAI and PPFD from measurements in similar beech dominated forests in eastern Denmark (Madsen & Larsen 1997).

7.2.7 Data analyses
All measurements and qualitative scores were analysed using Excel and SAS (proc glm). The datasets from 1992 and 2002 were adapted in order to merge them for analyses. In this paper, only data from living trees in the western half of the permanent plot (strip 1-4) (4800 m²) are analysed and only profile drawing and RLI measurement from strip two are presented. The forest bog is not part of the analysed area.

7.3 Results

7.3.1 Changes in species composition and stem density
The number of trees increased from 244 to 261 within the 10-year period, corresponding to an increase from 508 to 543 trees/ha. The number of ash and oak remained stable while beech decreased with 10% from 161 to 145 trees and elm increased with 77% from 47 to 83 trees (table 7.1). Thus, the average increase in stem number (7%) is closely related to the almost doubled number of elm trees. The total recruitment is approximately double as high as the total mortality, respectively 57 new and 32 dead individuals.

In the early aggradation phase a characteristic change in the species composition from beech dominance to elm dominance took place (table 7.1). Of the recruitment in the 10-year period, 46 were elm, 10 were beech, and 1 spindle. This pattern was also found in the species composition of individuals with a dbh <5 cm but higher than 3 m. Here, 60 out of 65 individuals were elm, four were beech and one was elder.
Despite the change in species composition, the distribution of the trees according to developmental phases is nearly unchanged in the period (table 7.1). The three dominant species beech, elm, and ash each contribute to the structure of the forest in a specialised way (table 7.1 and figure 7.3). Slim ash trees dominate the early biostatic phase, spatially overlapping a massive cohort of beech in late aggradation. Beech is well represented in all the developmental phases and develops under the canopy of ash as described in the climax microsuccession by Emborg et al. (2000), see chapter 5 an figure 7.3: 0-10 m, 50-70 m and 120 m. Elm dominates the early aggradation phase, but is hardly represented in the later developmental phases.

### 7.3.2 Horizontal pattern - overlap of trees in different developmental phases

The height of the uppermost canopy layer varies from 2-40 m above the forest floor (figure 7.3) and is made up by a very fine-grained and heterogeneous mosaic of trees in different developmental phases. The mosaic has only changed a little during the 10-year period. Only areas, which were in one of the shorter phases in 1992 (degradation, innovation and partly early aggradation) or zones hit by disturbance regimes, such as the gap in the centre of the plot, have changed developmental phase. All phases are represented in the uppermost canopy layer (figure 7.2). Beneath the uppermost canopy layer trees in lower developmental phases form a varying number of sub-canopy layers. The spatial overlap of trees in different developmental phases results in a complex pattern varying from one to four canopy layers or even full-storied parts where the canopy is at all vertical levels without any indications of divided layers (figure 7.2 and 7.3, table 7.2).

### 7.3.3 Vertical stratification in relation to light in the understorey

During the 10-year period the dynamics in the vertical structure has been minimal. The average vertical extension growth is 0.9 m varying from more than four meters for some ashes in the early biostatic phase to no or negative growth. In some cases the negative growth may be an expression for the uncertain factor related to the measurement of height using a clinometer. Despite the relatively little overall vertical extension growth, the relative light intensity in the understorey has changed a lot.

Measurements of RLI in 2002 along the centreline of a 10 m x 120 m transect (1200 m²) show, that the dense beech layer (late aggradation) determines the relative light intensity. In 1992 the RLI in the understorey was <1% in the whole area except the southern 10 x 10 m. This area was in degradation and RLI here varied between 0.4 and 10.1%. In 2002 three zones with distinct structural qualities and significant different RLI readings in the understorey were distinguished.

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<tbody>
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<td>E. Aggradation</td>
<td>74 46</td>
<td>43 72</td>
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<td></td>
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<td></td>
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<td></td>
<td>118 119</td>
<td>118 119</td>
<td>48 46</td>
<td>48 46</td>
</tr>
<tr>
<td>L. Aggradation</td>
<td>72 75</td>
<td>4 10</td>
<td>9 5</td>
<td></td>
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<td></td>
<td>85 91</td>
<td>85 91</td>
<td>35 35</td>
<td>35 35</td>
</tr>
<tr>
<td>E. Biostatic</td>
<td>8 18</td>
<td>1</td>
<td>23 24</td>
<td></td>
<td></td>
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<td></td>
<td>31 43</td>
<td>31 43</td>
<td>16 16</td>
<td>16 16</td>
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<tr>
<td>L. Biostatic</td>
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<td>3 2</td>
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<td></td>
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<td>10 6</td>
<td>4 2</td>
<td>4 2</td>
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<tr>
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<td></td>
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<td></td>
<td></td>
<td>0 2</td>
<td>0 2</td>
<td>1 1</td>
<td>1 1</td>
</tr>
<tr>
<td>%</td>
<td>66 56</td>
<td>1 1</td>
<td>19 32</td>
<td>13 11</td>
<td>0 0</td>
<td>0</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>244 261</td>
<td>244 261</td>
<td>100 100</td>
<td>100 100</td>
</tr>
<tr>
<td>Total</td>
<td>161 145</td>
<td>3 2</td>
<td>47 83</td>
<td>32 29</td>
<td>1 1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>244 261</td>
<td>244 261</td>
<td>100 100</td>
<td>100 100</td>
</tr>
</tbody>
</table>
Figure 7.2 - Spatial arrangement according to the uppermost canopy layer and each of the six developmental phases for the studied area. The crown projection maps 40x120 m is ordered according to ecological cycle. From the bottom the innovation phase followed by early aggradation, late aggradation, early biostatic, late biostatic and degradation. The top map shows the spatial arrangement according to the uppermost canopy layer. The brightness of the colour follows the height of the canopy.

A: Spatial arrangement of the different developmental phases according to the characteristics of the uppermost canopy layer. All phases are represented in the studied plot. The position of the transect depicted in Fig 7.3 is marked.

B: Spatial arrangement of the degradation phase.

C: Spatial arrangement of the late biostatic phase (> 80 cm DBH)

D: Spatial arrangement of the early biostatic phase (> 25 m < 80 cm DBH)

E: Spatial arrangement of the late aggradation phase (15 - 25 m)

F: Spatial arrangement of the early aggradation phase (3 - 15 m)

G: Spatial arrangement of the innovation phase (20 cm - 3m)
Seedlings < 3 m were recorded both in the gap (i.e. innovation) and under canopy cover. The big patch is totally dominated by Fraxinus seedlings 20-100 cm, 10-100/m2. The scattered regeneration in the rest of the area is mostly suppressed Ulmus (83) and Fagus (10), supplemented by shrubs Sambucus (9), Sorbus aucuparia (2) and Corylus avellana (1).
The first zone from 0-37 m is very heterogeneous both in structure and in RLI. This zone consists of three parts with less different RLI readings indicating the effect of sidelight coming from the neighbouring gap to the south. The second zone from 37-50 is a gap formed by the break down of a beech. In this zone the RLI is very high (14%). In the third zone from 50-120 a very dense canopy of beech in late aggradation is the uniting structural element causing a very low RLI (< 2%) in the understorey. Even though the gap is to the northern part of the transect the RLI readings are clearly higher in a 10 m zone from the gap. (table 7.2, figure 7.3).

Figure 7.3 (See next page) - Three representations from a north south orientated transect, 10 x 120 m. At the top a profile diagram showing the vertical structure (stratification) in May 2002. The position of the transect is marked on Fig. 7.2A. In the middle a diagram with RLI readings from the centreline of the transect, as they were in September 2002. Lowest a crown projection map showing the horizontal structure (pattern) in May 2002.
Table 7.2 - Structural analyses of the 10x120 transect depicted in figure 7.3

1 Full-storied (‘full-skiktning’) is a term for structural units, where the canopy is at all vertical level without any indications of divided layers, used by Gustavsson 1986.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Part</th>
<th>Canopy-layers</th>
<th>Developmental phase 2002</th>
<th>Developmental phase 1992</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1</td>
<td>2-4</td>
<td>Early bio./ Late agg.</td>
<td>Early bio./ Late agg.</td>
<td>A more or less homogenous canopy layer of beech with flat crown tops is the uniting structural element. The smaller beech at 10 m has lost the competition to a beech standing in front of but overlapping the shown transect. From 0-8 m slim ash trees in early biostatic make up a higher, clearly separated canopy layer. Umbrella shaped elm trees up to 7 m height form a scattered understorey. The slim ash has not grown higher in the 10-year period, neither has the beech.</td>
</tr>
<tr>
<td>B</td>
<td>2</td>
<td>Early bio.</td>
<td>Early bio.</td>
<td></td>
<td>The uppermost canopy layer is from a 34 m high (30 m in 1992) beech in early biostatic standing in front of but overlapping the shown transect. The sub-canopy layers are continuations from part A.</td>
</tr>
<tr>
<td>C</td>
<td>2</td>
<td>Early bio.</td>
<td>Early bio.</td>
<td></td>
<td>The beech in early biostatic standing in front of the shown transect forms the uppermost canopy layer. Except the area beneath more or less solitary shrub-shaped beech at 36 m, the forest floor is covered by regeneration of ash 20-100 cm high, 10-100/m². The innovation of ash is not shown on the profile.</td>
</tr>
<tr>
<td>D</td>
<td>1</td>
<td>Inno / Early agg.</td>
<td>Late bio.</td>
<td></td>
<td>The break down of the beech at 44 m in the December gale 1999 formed this gap. In 1992 this beech were 32,5 m high and were 108 cm DBH. The umbrella shaped elm and the beech at 36 m had established as suppressed understorey prior to the creation of the gap. Now the elm are covering and shading most of the forest floor spreading long branches like an umbrella. The forest floor is covered by dense regeneration of ash.</td>
</tr>
<tr>
<td>E</td>
<td>2</td>
<td>Early bio.</td>
<td>Late agg. Early bio. Late bio</td>
<td></td>
<td>The uniting structural element is a very dense and homogeneous canopy layer of beech in late aggradation. This layer was also in late aggradation in 1992, and has in average added ca. 1 m to the height. From 50-75 m slim ash trees in early biostatic form a higher, clearly separated canopy layer. These Fraxinus have grown ca. 4 m in height since 1992. From 75-107 m two oak in late biostatic form the uppermost canopy layer, the southern one standing in front of, but overlapping the shown transect. The forest floor is partly naked resulting in a relatively high room (ca. 8 m) beneath the canopy. The understorey is very scattered except from the southern part (107-120 m), which was in degradation in 1992. The ruins of degraded beech refer to the former generation. The suppressed individuals now couth under the dense canopy of beechestablished during this degradation phase. From 107-120 m a slim ash in early biostatic forms the uppermost canopy. The canopies are more or less united forming a full-storied unit, where the canopy is at all vertical level without any indications of divided layers¹.</td>
</tr>
</tbody>
</table>

Table 7.3 - Test of correlation between RLI and vertical structure of strip 2, dividing the strip into 5 zones

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of squares</th>
<th>Mean square</th>
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<tbody>
<tr>
<td>Model</td>
<td>4</td>
<td>204.41</td>
<td>51.10</td>
</tr>
<tr>
<td>Error</td>
<td>52</td>
<td>201.24</td>
<td>3.87</td>
</tr>
<tr>
<td>Corrected total</td>
<td>56</td>
<td>405.66</td>
<td></td>
</tr>
</tbody>
</table>

F-value | Pr > F | R-square |
<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>13.20</td>
<td>&lt; 0.0001</td>
<td>0.51</td>
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</tbody>
</table>

Least significant difference (LSD): Comparisons significant at the 0.05 level are indicated by ***.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Sum of squares</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
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<td>3.87</td>
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<tr>
<td>Corrected total</td>
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<td>405.66</td>
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F-value | Pr > F | R-square |
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<td>&lt; 0.0001</td>
<td>0.51</td>
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</table>

Least significant difference (LSD): Comparisons significant at the 0.05 level are indicated by ***.
7.4 Discussion
The study of the structural dynamics on a single-tree level using profile diagram and crown projections shows a very fine-grained mosaic with spatial overlap of trees at different height (developmental phases) results in a complex structure, which varied through the examined plot.

7.4.1 Change in species composition?
The increased values of RLI 1 m above the forest floor can be regarded as the main reason to the massive recruitment of elm at the expense of beech. Elm trees have thus established in the southern part of the plot, which in 1992 contained a gap. Presently, elms (both new individuals dbh >5 cm dbh and smaller saplings <5 cm dbh, but taller than 3 m height) are establishing in the northern part of the plot, where the collapse of two beech trees (in the late biostatic phase) under the 1999-storm created a canopy gap. The elms have reacted on the increased RLI by spreading an umbrella of long branches, shading the forest floor. This results in a very low establishment of beech (figure 7.3). The ability of elm to shoot from the basis and thereby having a much faster reaction to changed light condition than trees which have to sprout from seeds as beech may also have affected the recruitment. The differences in seed production between elm and beech may also affect the recruitment. The wind dispersed elm seeds are easily spread every year compared with the heavy beechnuts, which are only produced in mast years. Dutch Elm Disease may also indirectly affect the recruitment of elm by initiation of shoot from the basis.

7.4.2 Expansion of neighbouring crowns
Horizontal crown expansion or even changed growth direction of the stems have closed the 1992-gap and caught the regeneration under a rather dense and homogeneous canopy layer. The beech trees from 100-105 m on figure 7.3 have characteristic asymmetric crowns, with long branches stretching to the south and closing the former gap. Some of the trees even have stems that slant in the direction of the former gap. This characteristic horizontal crown expansion is a clear example of what has been discussed in chapter 5.

7.4.3 Canopy density determining the relative light intensity in the understorey
The changes in relative light intensity during the 10-year period indicates that RLI in the understorey is more influenced by the homogeneity and density of the canopy, than the height or number of canopy layers or the developmental phase of the uppermost canopy layer. The gap (figure 7.3, 37-50 m) in the canopy layer entails very heterogeneous RLI readings in the neighbouring areas. This neighbouring impact seems to be related to the geographic position. The impact on areas north and north-west to a gap is very high and on the same time affecting a wide zone (whole zone 1 in the analysed transect (figure 7.3). Sunlight and diffuse light coming from the gap, reaching well under the crowns can explain this. The impact on the RLI readings in areas south and south-east of a gap is almost as high as to the north but affecting a much narrower zone. Only diffuse light from the gap is spreading under the crown cover and no direct sunlight. In areas, which had a very homogeneous and dense canopy in both 1992 and 2002, the RLI readings are very low and almost identical even though the total number of canopy layers and the developmental phase of the uppermost canopy layer have changed.

7.4.4 An oak-canopy leads to a gradual take over from the understorey
The zone where oak dominates the uppermost canopy layer (figure 7.3, 72-105 m) seems not to follow the system of the cyclic development at all. The vital sub-canopy of beech in late aggradation and early biostatic will gradually take over when the oak trees loose major branches or die. Such areas will go directly from late biostatic to early biostatic as discussed in chapter 5.

7.4.5 Early-early biostatic and flash back to late aggradation
In nearly all areas with early biostatic phase in 2002, slim ash trees form the uppermost canopy layer. As an explicit example of the described climax microsuccession from ash to beech (Emborg et al. 2000), beech in late aggradation grows beneath the canopy of those ashes. Very often the ash crowns are clearly separated from the lower beech layer (figures 7.3: 0-8 m, 50-77 m, 115-120 m). In the future, beech will take over the canopy control, either by growing through the light canopy of the ash trees, or because of the degradation of the ashes due to their shorter lifecycle compared with beech. When the ash trees degrade a ‘flashback’ from early biostatic to late aggradation may be seen if the beech layer has not yet reached 25 m height. The degradation
of ash will moreover lead to a dramatic change in the forest picture during the remaining part of the biostatic phase. This indicates two clearly different phases within the early biostatic phase. An “early-early” biostatic phase where slim ashes form the uppermost canopy layer and beech forms a lower layer and a “late-early” biostatic where beech either has grown through the ash canopy or the ash trees have degraded and therefore beech form the uppermost canopy layer.
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Danish Research Council project SpyNatForce

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P. W. S. Errboes Foundation
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